

Four new species of *Russula* subsect. *Cyanoxanthinae* from China (Russulales, Russulaceae)

Yanliu Chen^{1*}, Bin Chen^{1,2*}, Ruoxi Liang³, Shengkun Wang¹, Mengya An¹, Jinhua Zhang¹, Jingying Liang⁴, Yaxin Wang¹, Xuelian Gao¹, Junfeng Liang¹

¹ Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangzhou 510520, China

² Institute of Biological and Medical Engineering, Guangdong Academy of Sciences, Guangzhou 510316, China

³ Honors College, Northwestern Polytechnical University, Xi'an, 710129, China

⁴ Longyandong Forest Farm of Guangdong Province, Guangzhou 510520, China

Corresponding author: Junfeng Liang (jfliang2000@163.com)

Abstract

Four new species of *Russula* subsect. *Cyanoxanthinae*, viz. *Russula atrochermesina* Y.L. Chen & J.F. Liang, *R. lavandula* Y.L. Chen, B. Chen & J.F. Liang, *R. lilaceofusca* Y.L. Chen & J.F. Liang and *R. perviridis* Y.L. Chen, B. Chen & J.F. Liang, from China are proposed, based on morphological and molecular evidence. *Russula atrochermesina* can be distinguished by its violet pileus with tuberculate-striate margin, distant lamellae that stain greyish-yellow when bruised, basidiospores ornamented by isolated warts, wide hymenial cystidia on lamellae edges, cystidia content negative reaction in sulphovanillin and branched subterminal cells in pileipellis. *Russula lavandula* has a purplish-white to violet red pileus with a yellow centre, frequently present lamellulae and furcations, stipe often with pale yellow near the base, isolated basidiospores ornamentation and unbranched cuticular hyphal terminations, while *R. lilaceofusca* is characterised by its lilac brown to dark brown pileus, crowded lamellae with lamellulae and furcations, stipe often turning reddish-yellow when bruised, subreticulate basidiospores ornamentation and clavate hymenial cystidia often with capitate appendage whose contents that change to reddish-black in sulphovanillin. *Russula perviridis* is characterised by its large basidiomata, smooth pileus surface, frequently present lamellulae and furcations, stipe with yellow-brown tinge, globose to broadly ellipsoid basidiospores with subreticulate ornamentation, long hymenial cystidia that turn greyish-black in sulphovanillin and symbiotic with *Quercus semecarpifolia*. Phylogenetic analyses, based on multi-gene ITS+LSU+mtSSU+*rpb2*, indicate that *R. atrochermesina*, *R. lavandula*, *R. lilaceofusca* and *R. perviridis* are closely related to *R. pallidirosea* and *R. purpureorosea*, *R. banwatchanensis*, *R. lakhanpalii* and *R. nigrovirens*, respectively.

Key words: Ectomycorrhiza, edible fungi, morphology, new species, phylogeny

Introduction

Russula Per. is amongst the most ecologically and economically important groups of macrofungi (Looney et al. 2018; Caboň et al. 2019). More than 800 valid species in the genus have been described, but this figure is far below the 2,000 estimated species number (Adamčík et al. 2019). *Russula* is currently



This article is part of:

Diversity, taxonomy, and systematics of macrofungi from tropical Asia

Edited by Olivier Raspé, Rui-Lin Zhao, Jennifer Luangsa-ard

Academic editor: Olivier Raspé

Received: 18 March 2024

Accepted: 1 July 2024

Published: 11 July 2024

Citation: Chen Y, Chen B, Liang R, Wang S, An M, Zhang J, Liang J, Wang Y, Gao X, Liang J (2024) Four new species of *Russula* subsect. *Cyanoxanthinae* from China (Russulales, Russulaceae). MycoKeys 107: 21–50. <https://doi.org/10.3897/mycokeys.107.123304>

Copyright: © Yanliu Chen et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

* These authors contributed equally to this work.

divided into nine subgenera, viz. *Russula* subg. *Archaeae* Buyck and V. Hofst., *R.* subg. *Brevipedum* Buyck & V. Hofst., *R.* subg. *Compactae* (Fr.) Bon, *R.* subg. *Crassotunicatae* Buyck & V. Hofst., *R.* subg. *Cremeoohraceae* Buyck & X.H. Wang, *R.* subg. *Glutinosae* Buyck & X.H. Wang, *R.* subg. *Heterophyllidiae* Romagn., *R.* subg. *Malodora* Buyck & V. Hofst. and *R.* subg. *Russula* Pers. (Buyck et al. 2018; Buyck et al. 2020; Buyck et al. 2024). The subsect. *Cyanoxanthinae* Singer belongs to *R.* subg. *Heterophyllidiae* and is characterised by the following set of characters: medium to large basidiomata, lamellulae and furcations mostly present, mild to acrid context taste, white to cream spore print, basidiospores with inamyloid suprahilar spots, metachromatic pileipellis in cresyl blue and mainly one-celled pileocystidia. In the wild mushroom markets in south-western China, mushrooms known locally as “Mitangjun” have always been named as *R. cyanoxantha* (Schaeff.) Fr. However, they comprise several species that differ from *R. cyanoxantha*. The species diversity in this subsection has remained unresolved for a long time on the Asian continent, including in China. In the past decade, the number of new species described within this subsection from East and Southeast Asia has increased due to the use of DNA sequence information (Zhao et al. 2015; Zhang et al. 2017; Song et al. 2019; Ghosh et al. 2020; Khatua et al. 2021; Crous et al. 2022; Song 2022).

We aim to clarify the species diversity and geographical distribution of the genus *Russula* in China. From 2012 to 2023, several large-scale fungal surveys were conducted in different regions of China and some interesting specimens were collected. We conducted ITS analyses and found that they belong to the subsect. *Cyanoxanthinae* and are distinct from described species. Subsequently, through morphological comparisons and further multi-gene tree analyses, it was confirmed that they are new species. Here, we propose four new species and provide their morphological descriptions, related illustrations and molecular phylogenetic positions.

Materials and methods

Sampling and morphological studies

The specimens studied in this paper were collected and photographed from five subtropical provinces in China during 2012–2023. Samples were dried at 50 °C and deposited in the Herbarium of the Research Institute of Tropical Forestry, Chinese Academy of Forestry (RITF).

Macro-morphological features were described using detailed field notes and photographs of fresh basidiomata. Colour designations followed those in the Methuen Handbook of Color (Kornerup and Wanscher 1981). The description of microscopic morphological features followed the template of Adamčík et al. (2019). All micromorphological features were observed using a ZEISS Imager M2 microscope (Carl Zeiss AG, Oberkochen, Germany) with oil immersion lenses at a magnification of 1000×. Basidiospores were observed and measured in Melzer’s Reagent in side view excluding ornamentation. Other microscopic structures were pretreated in 5% potassium hydroxide (KOH) and then stained with 1% Congo red solution. The pileipellis was examined in cresyl blue for the presence of ortho- or metachromatic reactions (Buyck 1989). Sulphovanillin (SV) was used to determine variation in the cystidia content (Caboň et al.

2017). Measurements of basidiospores are expressed as (Min–)AV–SD–AV–AV+SD(–Max), where Min = the minimum value, Max = the maximum value, AV = average, SD = standard deviation and Q stands for the length/width ratio of the basidiospores. A scanning electron microscope (SEM. JEOL JSM-SU8020) was used to illustrate the structure and ornamentation of the basidiospores.

DNA extraction, amplified and sequenced

A rapid extraction kit for fungal DNA (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to extract total DNA from dried specimens. A total of four nuclear loci including ITS (internal transcribed spacer region of ribosomal DNA), LSU (ribosomal nuclear large subunit), mtSSU (ribosomal mitochondrial small subunit) and *rpb2* (second largest subunit of RNA polymerase II) were amplified and sequenced. The ITS regions were amplified with the ITS1/ITS4 primer pairs (White et al. 1990). The LSU regions were amplified with the LR0R/LR5 primer pairs (Vilgalys and Hester 1990). The *rpb2* regions were amplified with the fRPB2-6F/fRPB2-7cR primer pairs (Matheny 2005). The mtSSU regions were amplified with the MS1/MS2 primer pairs (White et al. 1990). Amplifications were performed in 25 µl reactions containing 1.5 µl of Taq DNA polymerase (5U/µl, ThermoStable DNA polymerase, BBI), 5 µl of 5× PCR Buffer, 2.5 µl of dNTP (200 µmol/l), 3.5 µl MgCl₂, 1 µl of each primer (5 µmol/l), 2 µl of DNA template and 8.5 µl of ddH₂O.

The thermal cycling conditions for ITS, LSU, *rpb2* and mtSSU included an initial denaturation at 95 °C for 5 min, followed by 35 cycles of 95 °C for 30 s (denaturation); 53 °C for 30 s (ITS), 55 °C for 45 s (LSU), 54 °C for 45 s (mtSSU), 56 °C for 1 min (*rpb2*) (annealing), 72 °C for 1 min (elongation) and a final extension at 72 °C for 10 min. PCR products were purified using Bioteke's Purification Kit (Bioteke Corporation, Beijing, China) and sequenced with an ABI 3730 DNA analyser using an ABI BigDye 3.1 terminator cycle sequencing kit (Shanghai Sangon Biological Engineering Technology and Services Co., Ltd., Shanghai, China). The newly-generated sequences have been submitted to the GenBank database. All sequences used in this study are shown in Table 1.

DNA sequence alignments and molecular phylogenetic analyses

Representative sequences of species belonging to the subsect. *Cyanoxanthinae* were obtained from the GenBank database, based on recent published studies (Crous et al. 2022; Song 2022). Two species of subsect. *Substriatinae*, *R. maguanensis* J. Wang, X.H. Wang, Buyck & T. Bau and *R. substriata* J. Wang, X.H. Wang, Buyck & T. Bau, were used as outgroups. Sequences of four genes were aligned separately using MAFFT 7.0 (<http://mafft.cbrc.jp/alignment/server/>) and the alignment was manually refined using BioEdit v.7.0.9 (Hall 1999).

Phylogenetic analyses, based on a multi-gene matrix, were conducted using both Randomised Accelerated Maximum Likelihood (RAxML) and Bayesian Inference (BI). A partition homogeneity test (PHT) was performed using heuristic searches with PAUP* 4.0a (Swofford 2003) to evaluate incongruence amongst individual genes. The sequences were then concatenated using Phyutility v.2.2 (Smith and Dunn 2008) for multi-gene analyses as no supported conflicts ($P < 0.5$). The final aligned dataset was submitted to TreeBASE (31001).

Table 1. GenBank accession numbers for sequences used in this study. The newly-generated sequences are labelled in bold; holotypes are labelled by letter T in parentheses.

Taxon	Voucher	Location	NCBI. No				References
			ITS	LSU	<i>rpb2</i>	mtSSU	
<i>R. atrochermesina</i>	RITF6878 (T)	Yunnan, south-western China	OR907106	OR907057	OR914538	OR934536	This study
<i>R. atrochermesina</i>	RITF6460	Yunnan, south-western China	OR907107	OR907056		OR934535	This study
<i>R. banwatchanensis</i>	BBH 49228 (T)	Thailand	MT940813	MT940823	MT965687		Crous et al. (2022)
<i>R. cyanoxantha</i>	UE29.09.2002-2	France	DQ422033	DQ422033	DQ421970		Buyck et al. (2008)
<i>R. cyanoxantha</i>	FH 12–201	Germany	KR364093	KR364225	KR364341		De Crop et al. (2017)
<i>R. dinghuensis</i>	K15052704 (T)	Guangdong, southern China	KU863581	MK881922		MK882050	Zhang et al. (2017)
<i>R. dinghuensis</i>	RITF6860	Guangdong, southern China	OR907119	OR907061	OR914549	OR934507	This study
<i>R. dinghuensis</i>	RITF5885	Guangdong, southern China	OR907120		OR914550	OR934503	This study
<i>R. dinghuensis</i>	RITF5142	Jiangxi, central China	OR907123	OR907058	OR914551	OR934502	This study
<i>R. dinghuensis</i>	RITF6855	Guangxi, southern China	OR907121	OR907060	OR914552	OR934504	This study
<i>R. dinghuensis</i>	RITF6740	Guangxi, southern China	OR907122	OR907059	OR914553	OR934506	This study
<i>R. dinghuensis</i>	RITF6859	Guangdong, southern China	OR907124	OR907062	OR914554	OR934505	This study
<i>R. flavobrunnea</i> var. <i>violaceotincta</i>	71/BB 06.050	Madagascar		KU237468	KU237754	KU237312	Buyck et al. (2018)
<i>R. fusiformata</i>	K15052703 (T)	Guangdong, southern China	MK049978	MK881942		MK882070	Song (2022)
<i>R. fusiformata</i>	RITF6671	Zhejiang, eastern China	OR907108	OR907049	OR914567	OR934501	This study
<i>R. fusiformata</i>	RITF6487	Jiangxi, central China	OR907109		OR914563	OR934500	This study
<i>R. lakhanpalii</i>	CAL 1795 (T)	India	NR_173867				
<i>R. lakhanpalii</i>	RITF2600	Hubei, central China	OR907090	OR907076		OR934525	This study
<i>R. lakhanpalii</i>	RITF6973	Yunnan, south-western China	OR907089		OR914542	OR934526	This study
<i>R. lakhanpalii</i>	RITF6868	Yunnan, south-western China	OR907091	OR907078	OR914543	OR934528	This study
<i>R. lakhanpalii</i>	RITF6474	Yunnan, south-western China	OR907092	OR907077	OR914544	OR934527	This study
<i>R. lakhanpalii</i>	RITF6940	Yunnan, south-western China	OR907088	OR907079		OR934529	This study
<i>R. langei</i>	450/BB 07.792	France		KU237510	KU237796	KU237356	Buyck et al. (2018)
<i>R. lavandula</i>	RITF6329	Yunnan, south-western China	OR907083	OR907065	OR914534	OR934513	This study
<i>R. lavandula</i>	RITF6340	Yunnan, south-western China	OR907085	OR907066	OR914535	OR934515	This study
<i>R. lavandula</i>	RITF3196	Yunnan, south-western China	OR907086	OR907067		OR934512	This study
<i>R. lavandula</i>	RITF3282 (T)	Yunnan, southwestern China	OR907087	OR907068	OR914537	OR934511	This study
<i>R. lavandula</i>	RITF6349	Yunnan, south-western China	OR907084	OR907069	OR914536	OR934514	This study
<i>R. lilaceofusca</i>	RITF6330 (T)	Yunnan, south-western China	OR907102	OR907075	OR914539	OR934530	This study
<i>R. lilaceofusca</i>	RITF2645	Hubei, central China	OR907093	OR907074	OR914540	OR934531	This study
<i>R. lilaceofusca</i>	RITF2631	Hubei, central China			OR914541		This study
<i>R. lilaceofusca</i>	RITF3761	Guizhou, south-western China	OR907094				This study
<i>R. lilacina</i>	MMCR00191	Thailand	MT940809	MT940819	MT965685		Crous et al. (2022)
<i>R. lotus</i>	HKAS79209 (T)	Guangdong, southern China	MG214688	MG214695			Li and Deng (2018)
<i>R. lotus</i>	RITF3330	Yunnan, south-western China		OR907050			This study
<i>R. maguanensis</i>	HKAS 102277 (T)	Yunnan, south-western China	MH724918	MH714537	MH939989		Wang et al. (2019)
<i>R. nigrovirens</i>	HKAS 55222 (T)	Yunnan, south-western China	KP171173				Zhao et al. (2015)
<i>R. nigrovirens</i>	RITF6408	Yunnan, south-western China	OR907095	OR907073	OR914568	OR934521	This study
<i>R. pallidirosea</i>	UTC 00274382 (T)	USA	NR_153259				Kropp (2016)
<i>R. perviridis</i>	RITF3131 (T)	Yunnan, south-western China	OR907098	OR907072	OR914548	OR934523	This study
<i>R. perviridis</i>	RITF2912	Xizang, western China	OR907100	OR907070	OR914547	OR934522	This study
<i>R. perviridis</i>	RITF6983	Yunnan, south-western China	OR907099				This study
<i>R. perviridis</i>	RITF6982	Yunnan, south-western China	OR907101	OR907071	OR914545	OR934524	This study
<i>R. perviridis</i>	RITF6734	Sichuan, south-western China			OR914546		This study
<i>R. perviridis</i>	RITF3143	Yunnan, south-western China	OR907097				This study
<i>R. perviridis</i>	RITF6790	Xizang, western China	OR907096				This study
<i>R. phloginea</i>	CNX530524068 (T)	Yunnan, south-western China	MK860701	MK860704		MK860708	Song et al. (2019)

Taxon	Voucher	Location	NCBI. No				References
			ITS	LSU	<i>rpb2</i>	mtSSU	
<i>R. phloginea</i>	RITF6904	Yunnan, south-western China	OR907113				This study
<i>R. phloginea</i>	RITF6905	Yunnan, south-western China	OR907116	OR907051	OR914555	OR934516	This study
<i>R. phloginea</i>	RITF6906	Yunnan, south-western China	OR907117	OR907055	OR914558	OR934520	This study
<i>R. phloginea</i>	RITF6907	Yunnan, south-western China	OR907114	OR907052	OR914556	OR934517	This study
<i>R. phloginea</i>	RITF6908	Yunnan, south-western China	OR907115	OR907054	OR914557	OR934518	This study
<i>R. phloginea</i>	RITF6914	Yunnan, south-western China	OR907118	OR907053	OR914559	OR934519	This study
<i>R. pseudocyanoxantha</i>	CUH AM177 (T)	India	NR_173166				Khatua et al. (2021)
<i>R. purpureorosea</i>	H17050506 (T)	Guangdong, southern China	MK049976	MK881941		MK882069	Song (2022)
<i>R. purpureorosea</i>	RITF6835	Guangdong, southern China	OR907104	OR907082	OR914565	OR934533	This study
<i>R. purpureorosea</i>	RITF6834	Guangdong, southern China	OR907103	OR907081	OR914566	OR934534	This study
<i>R. purpureorosea</i>	RITF5886	Guangdong, southern China	OR907105	OR907080	OR914564	OR934532	This study
<i>R. purpureoviridis</i>	BBH 49226 (T)	Thailand		MT940817	MT965684		Crous et al. (2022)
<i>R. subpallidirosea</i>	K15052818 (T)	Guangdong, southern China	KU863582	MK881923		MK882051	Zhang et al. (2017)
<i>R. subpallidirosea</i>	RITF3219	Yunnan, south-western China	OR907111	OR907063	OR914560	OR934508	This study
<i>R. subpallidirosea</i>	RITF3343	Yunnan, south-western China	OR907112		OR914562	OR934509	This study
<i>R. subpallidirosea</i>	RITF6264	Yunnan, south-western China	OR907110	OR907064	OR914561	OR934510	This study
<i>R. substriata</i>	HKAS 102278 (T)	Yunnan, south-western China	MH724921	MH714540	MH939992		Wang et al. (2019)
<i>R. variata</i>	BPL241	USA	KT933959	KT933818	KT933889		Looney et al. (2016)

A mixed-model (partitioned) scheme was used for ML and BI analyses, ITS, LSU, mtSSU and *rpb2*. The best-fit model of sequence evolution for each gene was estimated using MrModelTest 2.3 (Nylander 2004), based on the Akaike Information Criterion. The best model for the BI analysis of the ITS and LSU datasets was the GTR+I+G model; the SYM+G model was optimal for *rpb2*; and the GTR+I model was optimal for mtSSU. RaxML 7.0.3 (Stamatakis 2006) and MrBayes v.3.2 (Ronquist et al. 2012) were used to perform the RAxML and BI analyses, respectively. Maximum Likelihood analysis was conducted using non-parametric bootstrapping with 1,000 replicates. Bootstrap support (BS) above 70% (Nuhn et al. 2013) was considered significant. BI analysis was performed using the Metropolis-coupled Markov Chain Monte Carlo method. Four chains were run for 1,500,000 generations and trees were sampled every 100 generations. Other parameters were kept at their default settings. The analysis was terminated when the average standard deviation of the splitting frequency was below 0.01 and the PSRF values for all parameters were near 1. Bayesian posterior probabilities (BPP) were calculated after discarding the first 25% of the samples as burn-in and branches with BPP over 0.95 were considered significantly supported.

Results

Phylogeny

The four-gene dataset (ITS+LSU+mtSSU+*rpb2*) included 65 samples representing 22 species. The matrix contains a total of 2,786 nucleotide sites, including 652 ITS sites, 896 LSU sites, 516 mtSSU sites and 722 *rpb2* sites. The tree topologies of both the RAxML and BI analyses were similar and only the tree inferred by the ML analysis is displayed, but with both BS and BPP values (Fig. 1).

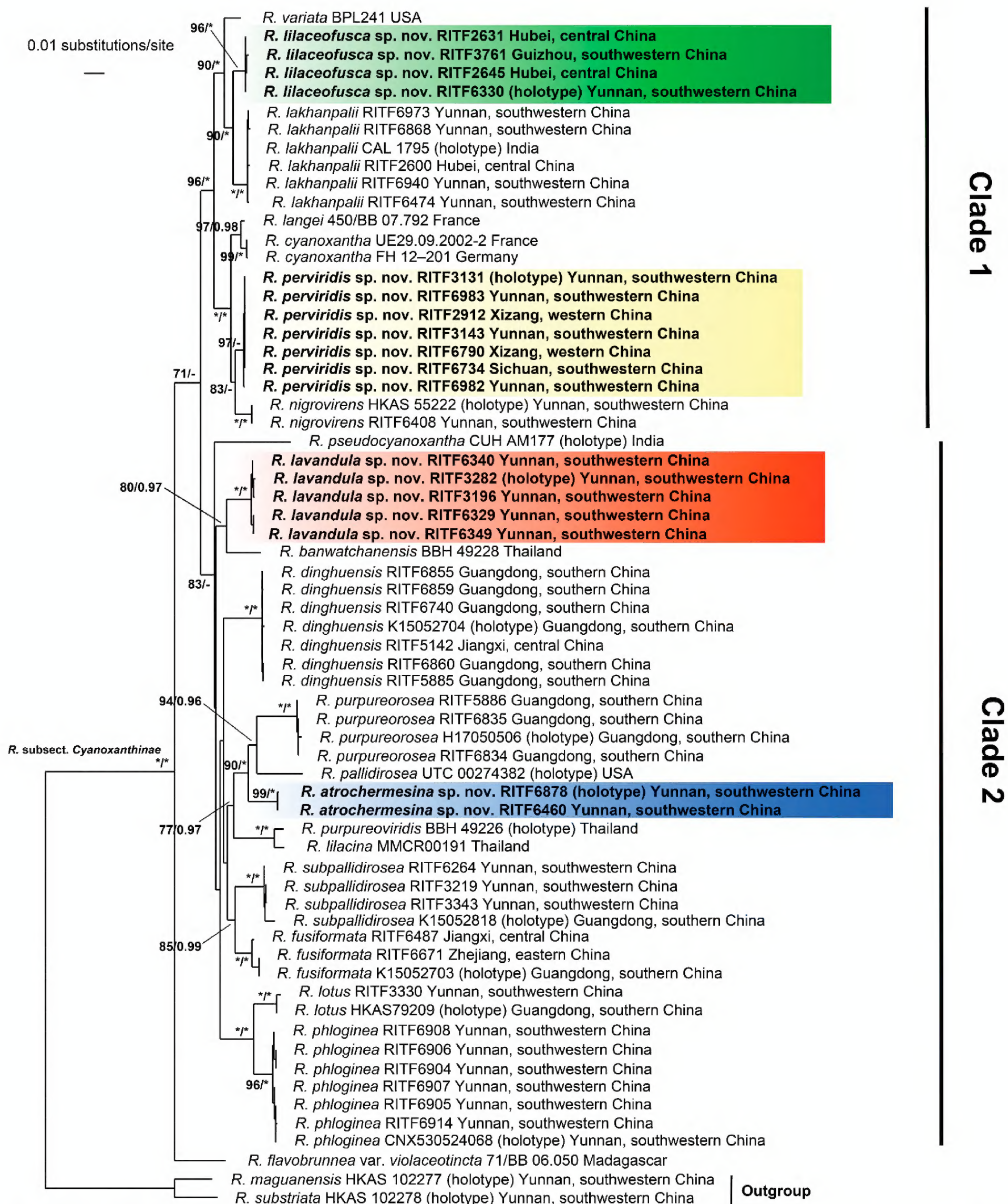


Figure 1. The RAXML likelihood tree based on the four-gene dataset (ITS+LSU+mtSSU+rpb2). Support values (BS > 70%, BPP > 0.95) are displayed above or below the branches, with the maximum values of BS (= 100%) and BPP (= 1.0) represented by asterisks (*). The four new species are marked with different colours.

Our molecular phylogenetic analyses show that *Cyanoxanthinae* can be divided into two major supported lineages and one species from Madagascar. All samples from China fell into major clades and represent 12 species, of which four are new species. The four new species proposed each formed a

well-supported branch and were distinct from other related taxa. *Russula atrochermesina* Y.L. Chen & J.F. Liang, sp. nov. (BS = 99%, BPP = 1.00) was closely related to *R. pallidirosea* Kropp and *R. purpureorosea* Y. Song. *Russula lavandula* Y.L. Chen, B. Chen & J.F. Liang, sp. nov. (100% BS and 1.00 BPP) was sister to *R. banwatchanensis* Sommai, Pinruan, Somrith. & Luangsa-ard (80% BS and 0.97 BPP). *Russula lilaceofusca* Y.L. Chen & J.F. Liang, sp. nov. (BS = 96%, BPP = 1.00) was allied to *R. lakhanpalii* (90% BS and 1.00 BPP). *Russula perviridis* Y.L. Chen, B. Chen & J.F. Liang, sp. nov. (BS = 97%, BPP < 0.95) was close to *R. nigrovirens* Q. Zhao, Y.K. Li & J.F. Liang (BS = 83%, BPP < 0.95).

Taxonomy

Russula atrochermesina Y.L. Chen & J.F. Liang, sp. nov.

MycoBank No: 851267

Figs 2A–C, 3A–D, 4, 5

Diagnosis. *Russula atrochermesina* can be distinguished by its violet pileus with tuberculate-striate margin, distant lamellae that stain greyish-yellow when bruised, wide hymenial cystidia on lamellae edges, cystidia content negative reaction in sulphovanillin, branched subterminal cells in pileipellis.

Holotype. CHINA, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Lufeng City, Tuoan Township, 25°14'35"N, 101°46'23"E, alt. 2250 m, 7 Sep 2023, Y.L. Chen (RITF6878).

Etymology. '*atrochermesina*' refers to the dark purple colour of pileus.

Description. *Basidiomata* medium to large-sized; pileus 75–115 mm in diameter, initially hemispherical when young, convex to applanate when mature, margin tuberculate-striate, not cracked; surface dry, glabrous, peeling readily, violet white (16A2) to pale violet (16A3), dark violet (16F6) in the centre. **Lamellae** adnate, 5–8 per cm near pileus margin, cream, staining greyish-yellow (2B5) when bruised; lamellulae present and irregular in length; furcations frequently present near the stipe; edge entire and concolorous. **Stipe** 80–170 × 25–40 mm, cylindrical to subcylindrical, white (1A1), often with yellowish-white (1A2) tinge, solid. **Context** white (1A1), unchanging when bruised, compact, 5 mm thick in half of the pileus radius; taste mild; odour inconspicuous. **Spore print** not observed.

Basidiospores (6.3–)6.7–7.2–7.6(–8.7) × (5.3–)5.8–6.2–6.5(–7.4) µm, Q = (1.05–)1.11–1.15–1.20(–1.25), subglobose to broadly ellipsoid, hyaline in 5% KOH; ornamentation of small to medium, dense (5–9 in a 3 µm diam. circle) amyloid warts, less than 0.6 µm high, mostly isolated or fused in pairs, occasionally fused by short lines; suprahilar plage inamyloid. **Basidia** (33.0–)37.0–43.0–48.5(–52.0) × (9.0–)10.0–11.5–12.5(–14.0) µm, clavate, 2- to 4-spored, thin-walled; basidiola clavate, ca. 8.0–12.5 µm wide. **Hymenial cystidia on lamellae sides** moderately numerous, (52.5–)55.0–60.5–65.5(–69.5) × (7.0–)8.0–8.5–9.5(–10.0) µm, fusiform, apically acute, usually with an appendage, thin-walled; contents heteromorphous, yellow in sulphovanillin. **Hymenial cystidia on lamellae edges** longer and wider than those on lamellae sides, (54.5–)58.0–65.0–71.5(–75.5) × (8.0–)9.0–10.5–11.5(–13.0) µm, fusiform, apically mostly acute, usually with an appendage, thin-walled; contents crystalline, yellow in sulphovanillin. **Marginal cells** undifferentiated. **Pileipellis** hyphae of

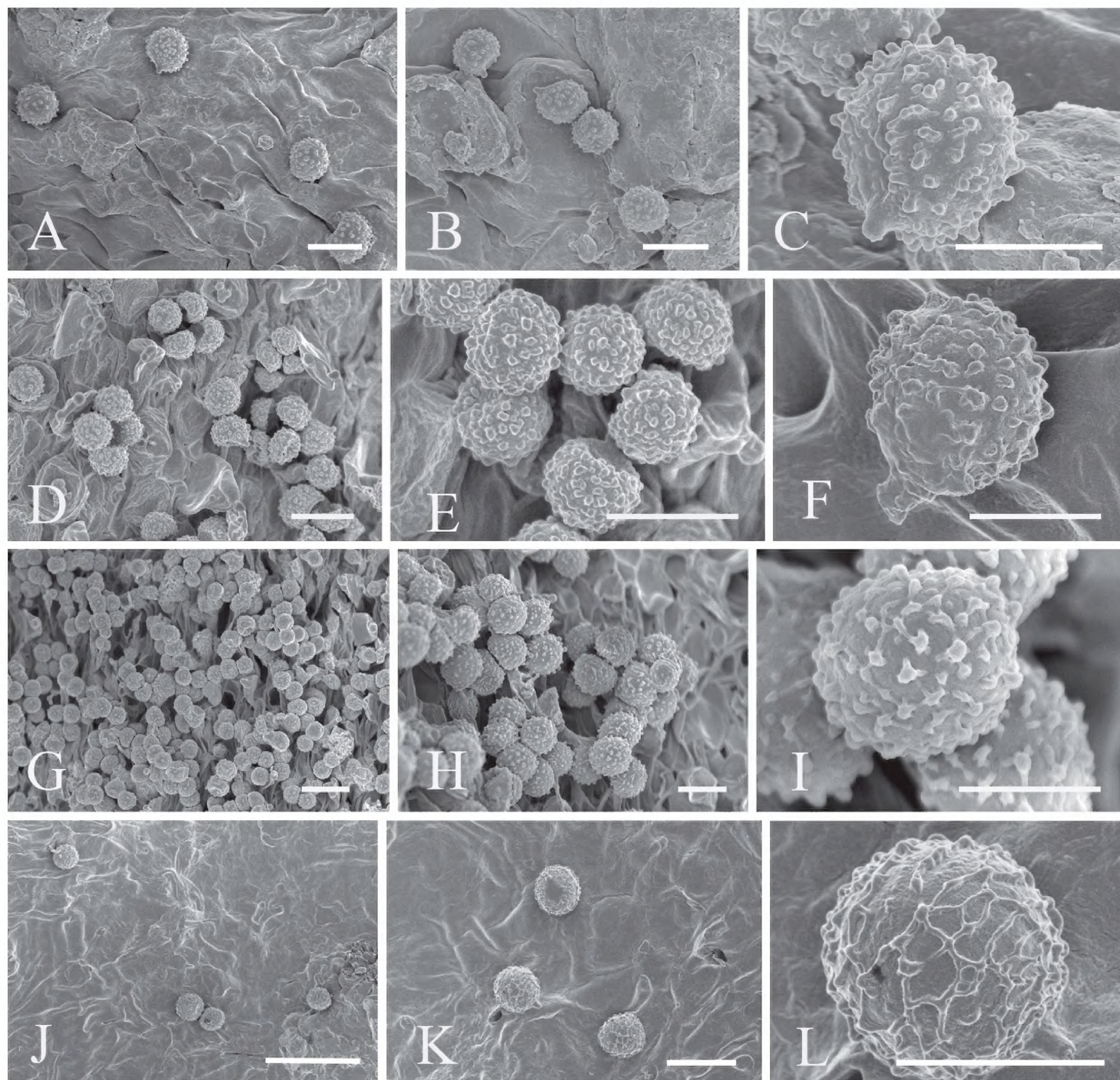


Figure 2. SEM photos of basidiospores of the four new species **A–C** *Russula atrochermesina* (RITF6878, holotype) **D–F** *Russula lavandula* (RITF6329) **G–I** *Russula lilaceofusca* (RITF6330, holotype) **J–L** *Russula perviridis* (RITF3131, holotype). Scale bars: 20 µm (**G**); 10 µm (**A, B, D, E, H, J, K**); 5 µm (**C, F, I, L**).

all tissues metachromatic in cresyl blue, sharply delimited from the underlying context, two-layered, gelatinised; suprapellis 260–400 µm deep, composed of densely arranged and erect hyphal terminations; subpellis 150–200 µm deep, composed of horizontally orientated and 2–9 µm wide hyphae. Hyphal terminations near the pileus margin branched, thin-walled; terminal cells (9.0–)13.5–18.0–22.5(–27.5) × (2.5–)3.5–4.0–5.0 µm, mainly clavate, occasionally cylindrical, apically mostly obtuse; subterminal cells usually shorter, ca. 3.0–5.5 µm wide, branched. Hyphal terminations near the pileus centre slightly narrower than those near the pileus margin; terminal cells (10.0–)13.5–17.5–21.5(–26.5) × (2.5–)3.0–3.5–4.0(–5.0) µm, cylindrical, slightly attenuated. **Pileocystidia** near the pileus margin always 1-celled, (22.5–)28.5–36.0–44.0(–50.0) × (4.0–)4.5–5.0–6.0(–6.5) µm, dispersed, clavate, occasionally fusiform,



Figure 3. Fruiting bodies photos of four new species **A–D** *Russula atrochermesina* (A–C–RITF6878, holotype, D–RITF6460) **E–I** *Russula lavandula* (E–F–RITF6329, G–H–RITF6340, I–RITF3282, holotype) **J–L** *Russula lilaceofusca* (J–K–RITF6330, holotype, L–RITF2631) **M–R** *Russula perviridis* (M–N–RITF3131, holotype, O–P–RITF6982, Q–R–RITF6983). Scale bars: 40 mm (A, B, D–G, I, J, M–O); 5 mm (C, L); 20 mm (H, K, P, Q, R).

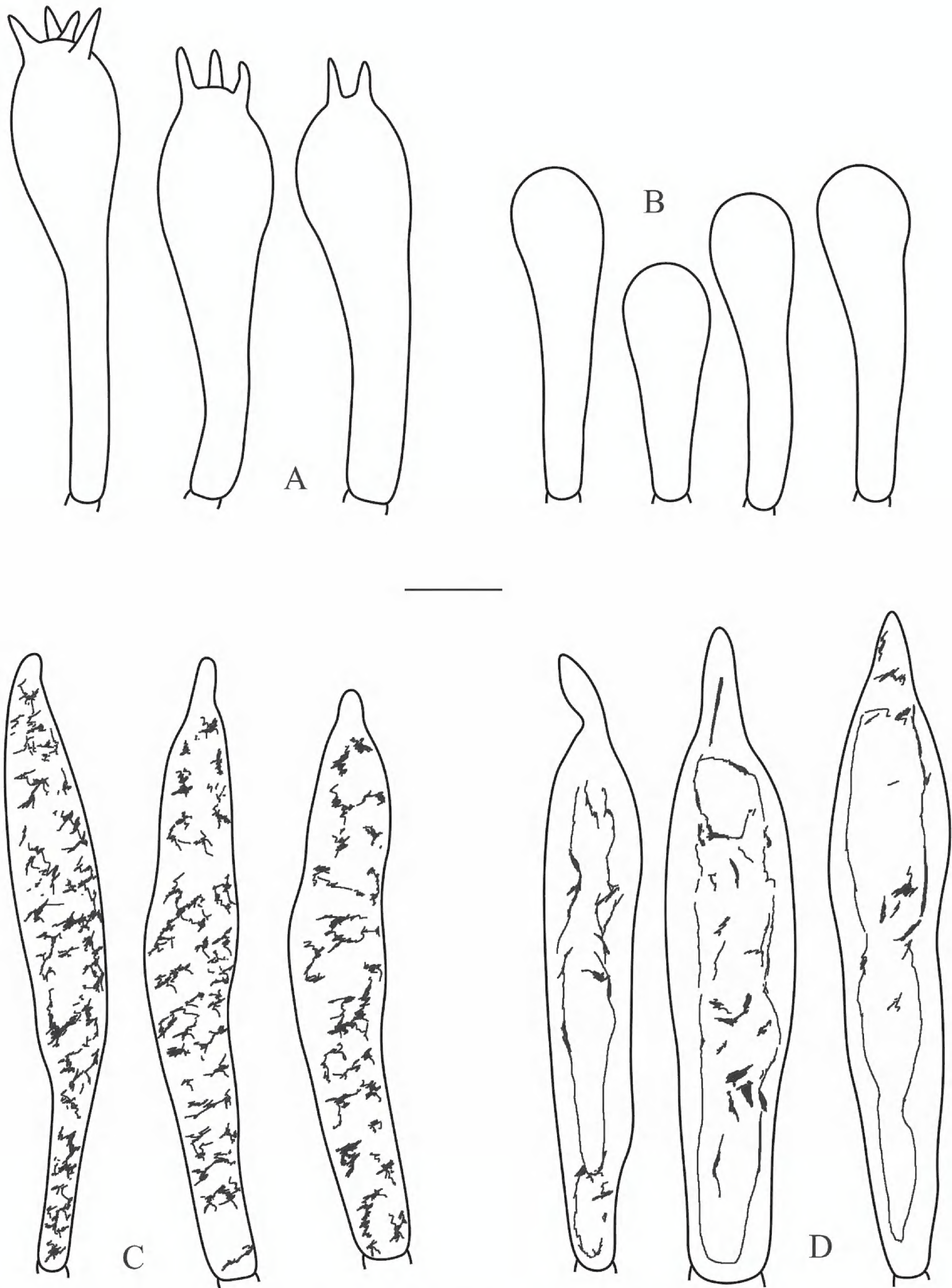


Figure 4. *Russula atrochermesina* (RITF6878, holotype) **A** basidia **B** basidiola **C** hymenial cystidia on lamellae sides **D** hymenial cystidia on lamellae edges. Scale bar: 10 μ m.

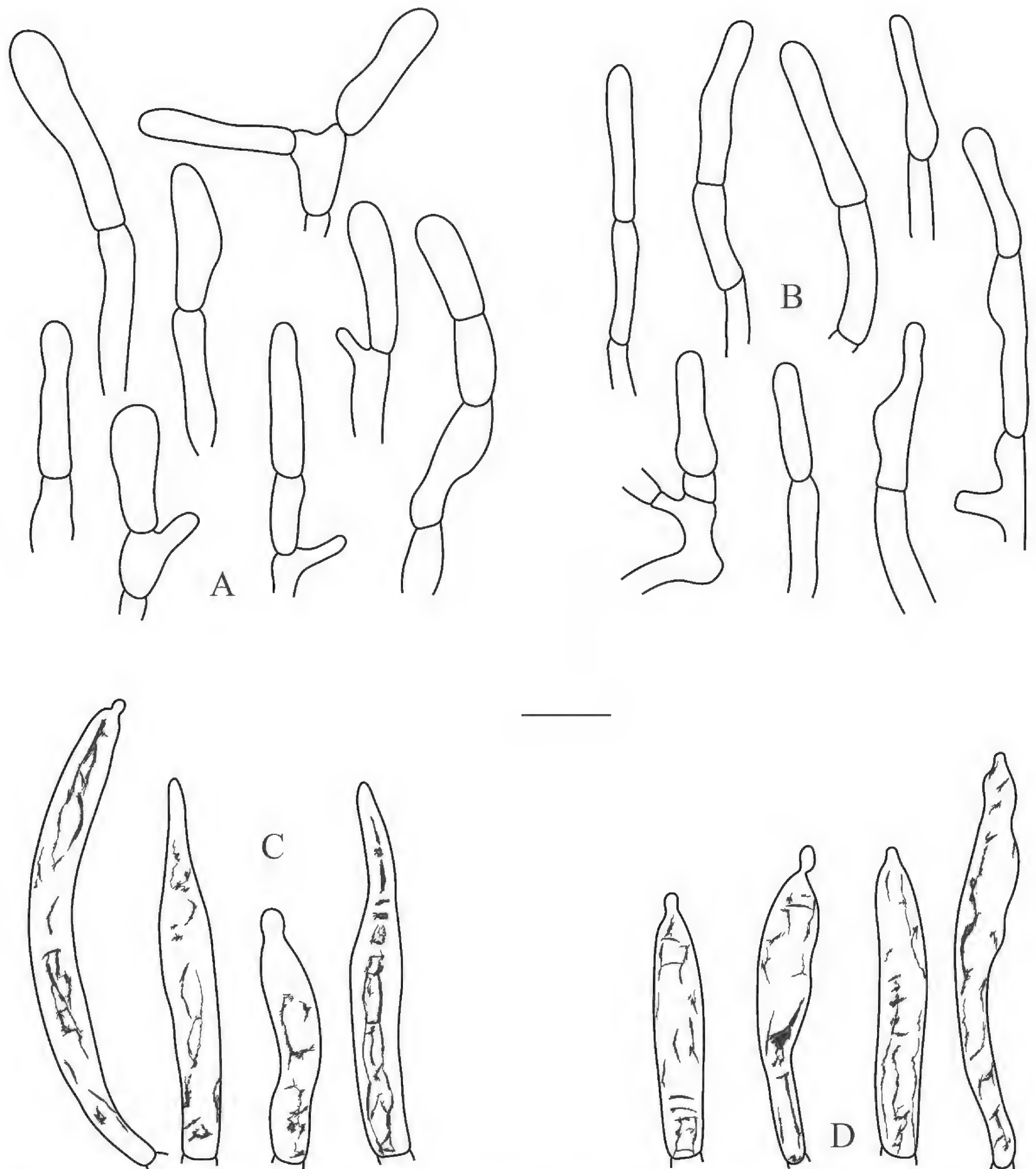


Figure 5. *Russula atrochermesina* (RITF6878, holotype) **A** hyphal terminations near the pileus margin **B** hyphal terminations near the pileus centre **C** pileocystidia near the pileus margin **D** pileocystidia near the pileus centre. Scale bar: 10 μm .

apically usually obtuse, sometimes with a round or elliptical appendage, thin-walled; contents crystalline, no reaction in sulphovanillin. Pileocystidia near the pileus centre slightly narrower than those near the pileus margin, (30.0–)32.0–38.0–44.0(–51.5) $\times$ (3.5–)4.0–4.5–5.0(–5.5) μm .

Habitat. On the ground under mixed forests dominated by *Castanopsis sclerophylla* and *Pinus yunnanensis*.

Known distribution. South-western China (Yunnan Province).

Additional specimens examined. CHINA, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Lufeng City, Tuoan Township, 25°14'34"N, 101°45'39"E, alt. 2300 m, 28 Jul 2022, X.L. Gao (RITF6460).

Notes. Phylogenetic analyses showed that *R. atrochermesina* is related to *R. pallidirosea*, *R. purpureorosea* and *R. purpureoviridis* Khamsuntorn, Lueangja-roenkit, Sommai & Pinruan. However, *R. pallidirosea* from American Samoa has a pallid to pinkish pileus and smaller hymenial cystidia on the lamellae edges (40.0–55.0 × 5.0–7.0 µm) and is associated with tropical trees (Kropp 2016). *Russula purpureorosea* differs in the following set of characters: pale pinkish-purple pileus, lamellae furcations absence, narrower hymenial cystidia on lamellae edges (54.0–60.0–95.0 × 7.0–8.5–10.0 µm) and unbranched hyphal terminations in the pileipellis (Song 2022). *Russula purpureoviridis*, originally described from Thailand, differs in a greyish-green pileus, narrower hymenial cystidia on lamellae edges (45.0–77.5 × 7.5–10.0 µm), constricted terminal cells in the pileipellis and larger pileocystidia (52.5–87.5 × 5.0–8.5 µm) (Crous et al. 2022). The morphology of *R. atrochermesina* is similar to *R. fusiformata*. However, *R. fusiformata* lacks lamellulae and furcations and has narrower hymenial cystidia on lamellae edges (35.5–52.0–78.0 × 5.0–9.0–11.0 µm) and shorter and wider terminal cells near the pileal centre (5.5–14.0 × 3.0–8.0 µm) (Song 2022).

***Russula lavandula* Y.L. Chen, B. Chen & J.F. Liang, sp. nov.**

MycoBank No: 851264

Figs 2D–F, 3E–I, 6, 7

Diagnosis. *Russula lavandula* is characterised by its purplish-white to violet red pileus with a yellow centre, frequently present lamellulae and furcations, stipe often with pale yellow near the base, isolated basidiospores ornamentation and unbranched cuticular hyphal terminations. It is mainly distinguished from *R. lotus* Fang Li by its frequently present lamellulae and furcations, subglobose to broadly ellipsoid basidiospores, moderately numerous and narrower hymenial cystidia on lamellae sides and shorter cuticular terminal cells.

Etymology. ‘*lavandula*’ refers to the colour of its pileus similar to lavender.

Holotype. CHINA, Yunnan Province, Kunming City, Wild Duck Lake, 25°07'34"N, 102°51'42"E, alt. 2100 m, 27 Jul 2014, H.J. Li (RITF3282).

Description. *Basidiomata* medium-sized; pileus 40–80 mm in diameter, initially hemispherical when young, convex to applanate with a depressed centre after maturity; margin incurved, striation short or inconspicuous, cracked after maturity; surface dry, glabrous, peeling readily, locally cracking into pale yellow (2A3), purplish-white (14A2) to greyish-magenta (13D5 or 14E6) patches, rose (13B3), purplish-white (14A2) to violet red (14B6), sometimes white (1A1) at the margin, yellowish-white (1A2) to golden yellow (4C7) in the centre. **Lamellae** adnate to slightly adnexed, 10–13 per cm near pileus margin, white (1A1), unchanging when bruised, 3–4 mm wide; lamellulae usually present and irregular in length; furcations frequently present throughout the lamellae; edge entire and concolorous. **Stipe** 40–60 × 16–25 mm, cylindrical, flexuous and tapering towards the base, white (1A1), often with pale yellow tinge near the base, solid.

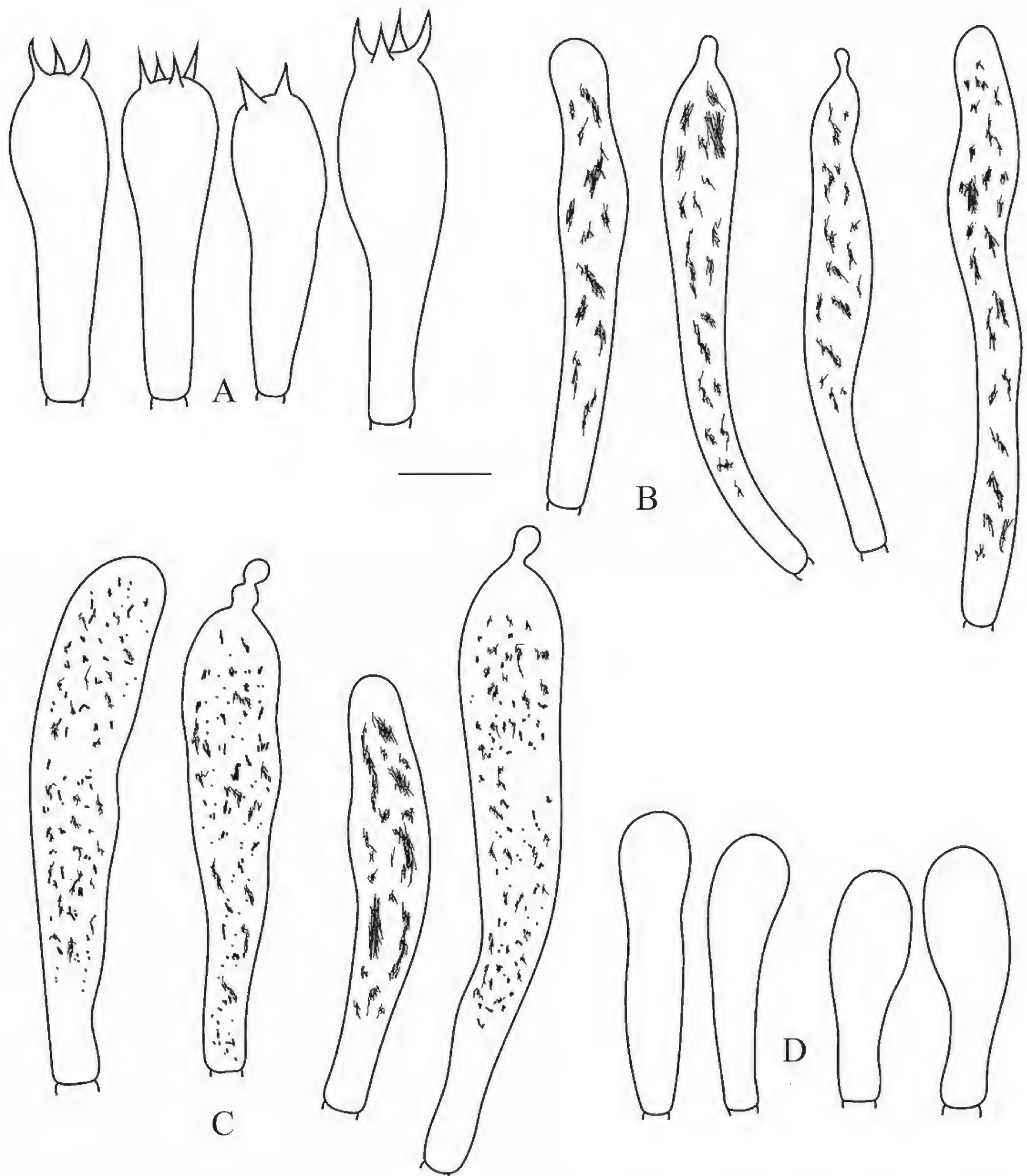


Figure 6. *Russula lavandula* (RITF3282, holotype) **A** basidia **B** hymenial cystidia on lamellae sides **C** hymenial cystidia on lamellae edges **D** basidiola. Scale bar: 10 μm .

Context white (1A1), unchanging when bruised, 3–4 mm thick in half of the pileus radius; taste mild; odour inconspicuous. **Spore print** not observed.

Basidiospores (6.5–)7.1–7.7–8.3(–9.2) $\times$ (5.9–)6.4–6.9–7.5(–8.0) μm , $Q = (1.01\text{--})1.05\text{--}1.11\text{--}1.17(1.24)$, subglobose to broadly ellipsoid, hyaline in 5% KOH; ornamentation of small, moderately distant to dense (6–8 in a 3 μm diam. circle) amyloid warts, less than 0.5 μm high, mostly isolated, occasionally connected by short line connections or ridges, not forming a reticulum;

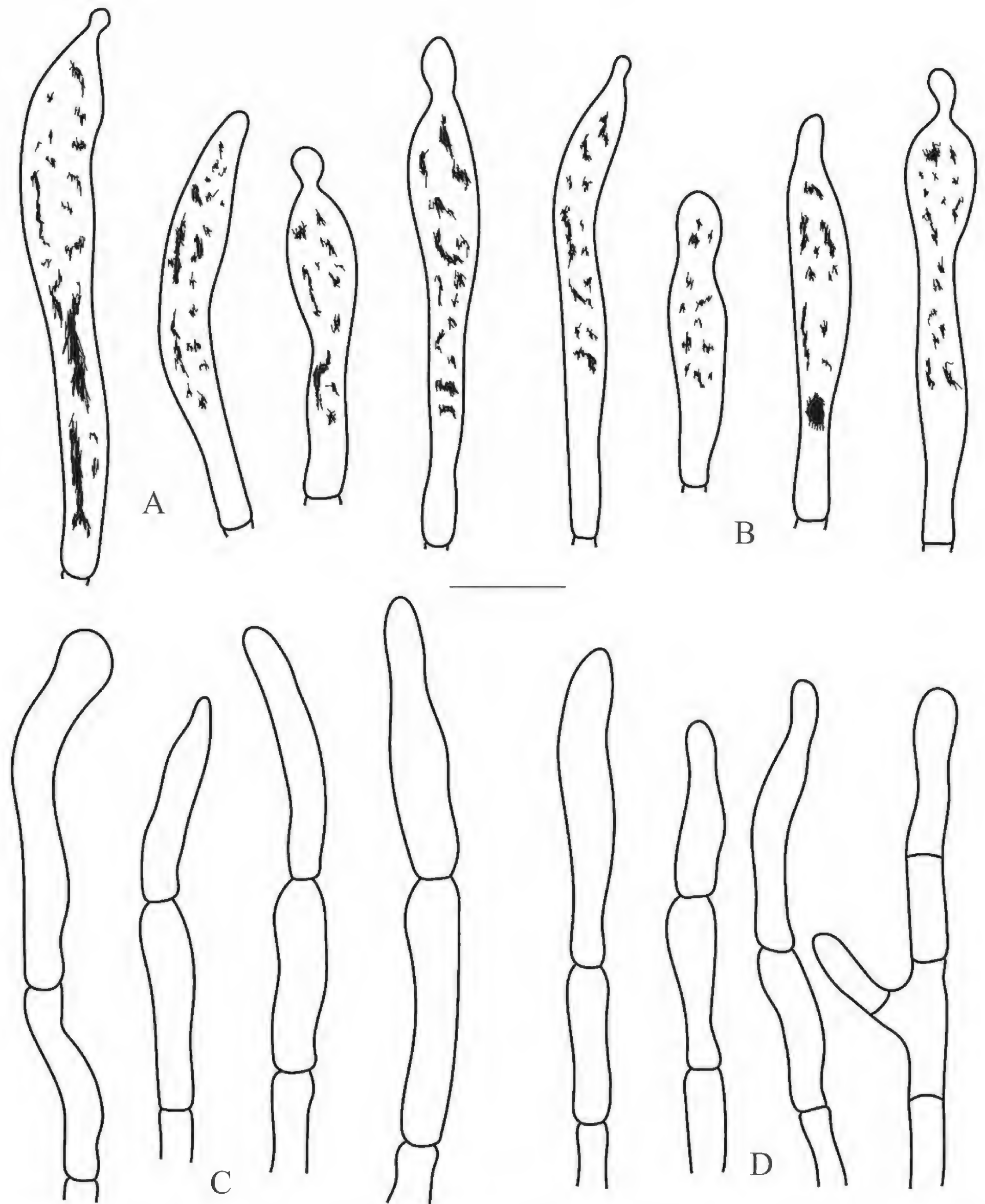


Figure 7. *Russula lavandula* (RITF3282, holotype) **A** pileocystidia near the pileus margin **B** pileocystidia near the pileus centre **C** hyphal terminations near the pileus margin **D** hyphal terminations near the pileus centre. Scale bar: 10 μm .

suprahilar plage indistinct, inamyloid. **Basidia** (24.0–)28.5–33.5–39.0(–43.5) $\times$ (6.0–)7.0–8.5–9.5(–10.5) μm , clavate, 2- to 4-spored, thin-walled; basidio-
la clavate or subcylindrical, ca. 5–10 μm wide. **Hymenial cystidia on lamellae**

sides moderately numerous, (42.5–)47.0–54.5–62.5(–64.5) × (5.0–)6.5–7.5–8.5 µm, clavate or fusiform, apically mostly obtuse, partially acute, sometimes with a 4–6 µm and papillate appendage, thin-walled; contents granulose or heteromorphous, reddish-black in sulphovanillin. **Hymenial cystidia on lamellae edges** shorter, but wider than those on lamellae sides, (35.0–)39.0–46.0–52.5(–56.0) × (6.0–)7.0–8.1–9.2(–10.0) µm, mostly clavate or subcylindrical, apically mostly obtuse, occasionally with 2–5 µm long, papillate or moniliform appendage. **Marginal cells** undifferentiated. **Pileipellis** only hyphae of suprapellis metachromatic in cresyl blue, sharply delimited from the underlying context, 300–450 µm deep, two-layered, gelatinised; suprapellis 180–200 µm deep, composed of densely arranged and prostrate to erect hyphal terminations; subpellis 140–260 µm deep, composed of horizontally orientated, intricate and 3–5 µm wide hyphae. Hyphal terminations near the pileus margin unbranched, thin-walled, occasionally flexuous; terminal cells (12.5–)14.5–19.5–24.5(–26.0) × 4.5–5.0–5.5(–6.5) µm, mainly cylindrical, occasionally lageniform, apically mostly obtuse; subterminal cells usually shorter and slightly wider, ca. 4–7 µm wide, unbranched. Hyphal terminations near the pileus centre shorter and narrower than those near the pileus margin; terminal cells (11.0–)13.5–17.0–20.5(–21.5) × (3.5–)4.0–4.2–4.5 µm, clavate or cylindrical, apically obtuse; subterminal cells usually wider, ca. 4–6 µm, unbranched. **Pileocystidia** near the pileus margin always 1-celled, (20.0–)27.0–36.0–45.0(–48.0) × 4.5–5.5–6.0(–6.5) µm, clavate, occasionally fusiform, apically usually obtuse, sometimes with 2–6 µm long, round or elliptical appendage, thin-walled; contents crystalline, reddish-black in sulphovanillin. Pileocystidia near the pileus centre similar to those near the pileus margin, (20.0–)26.0–36.0–45.5(–52.5) × 4.0–5.0–5.5(–6.0) µm.

Habitat. On the ground under mixed forests of *Pinus yunnanensis*, *Lithocarpus dealbatus* and *Quercus* spp.

Known distribution. South-western China (Yunnan Province).

Additional specimens examined. CHINA, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Lufeng City, Guangtong Town, 25°14'43"N, 101°45'53"E, 18 Sep 2022, X.L. Gao (RITF6329); *ibid*, 25°14'48"N, 101°45'28"E, alt. 2400 m, 24 Sep 2022, X.L. Gao (RITF6340); *ibid*, 25 Sep 2022, X.L. Gao (RITF6349); Kunming City, Wuhua District, Qiongzhu Temple, 25°3'58"N, 102°37'29"E, alt. 2150 m, 28 Jul 2012, Y.J. Hao (RITF3196).

Notes. *Russula lavandula* is phylogenetically related to Thai *R. banwatchanensis* and Indian *R. pseudocyanoxantha* Paloi, K. Acharya & S. Khatua (Fig. 1). However, *R. lavandula* can be easily distinguished from them by its cracked pileus. Moreover, *R. banwatchanensis* differs in its darker coloured pileus, lack of lamellulae, thick-walled basidia and often longer pileocystidia of 42.5–127.0 × 2.5–5.0 µm (Crous et al. 2022) and *R. pseudocyanoxantha* differs in its darker coloured pileus, lack of lamellae furcations and association with *Shorea robusta* (Khatua et al. 2021). *Russula lavandula* can be easily confused with four Chinese species, via. *R. lotus*, *R. phloginea* J. Song & J.F. Liang, *R. purpureorosea* and *R. subpallidirosea* J.B. Zhang and L.H. Qiu in the field. However, *R. lotus*, originally described from southern China, can be easily distinguished by its absence of lamellae furcations, broadly ellipsoid to ellipsoid basidiospores, dispersed and wider hymenial cystidia on lamellae sides (52.0–70.0 × 10.0–16.0 µm) and longer cuticular terminal cells (10.0–40.0 × 4.0–8.0 µm) (Li and

Deng 2018). *Russula phloginea*, which occurs in subalpine areas, differs in having lamellae furcations only present near the stipe, smaller basidiospores of $(6.0-6.5-8.0 \times 5.0-6.5 \mu\text{m})$, longer hymenial cystidia of $(48.0-60.0-78.5(-79.5) \times 7.5-9.5(-10.0) \mu\text{m})$ and pileocystidia with a moniliform apex (Song et al. 2019). *Russula purpureorosea* and *R. subpallidirosea*, can be distinguished from *R. lavandula* by their rosy brown, pale pinkish-purple or pale greyish-pink pileus centre and occurrence at low altitudes (Zhang et al. 2017; Song 2022). Besides, *R. purpureorosea* lacks lamellae furcations and has shorter terminal cells of the pileipellis $(6.5-15.5 \times 2-5.5 \mu\text{m})$ and wider pileocystidia $(17.0-53.0 \times 4.5-9.0 \mu\text{m})$ (Song 2022). In addition, *R. cyanoxantha*, can be confused with *R. lavandula*. However, *R. cyanoxantha* can be distinguished by its uncracked pileus cuticle, longer hymenial cystidia up to $100 \mu\text{m}$ and slender cuticular hyphal end cells of $2-3 \mu\text{m}$ (Bon 1988; Sarnari 1998).

***Russula lilaceofusca* Y.L. Chen & J.F. Liang, sp. nov.**

MycoBank No: 851265

Figs 2G–I, 3J–L, 8, 9

Diagnosis. *Russula lilaceofusca* is mainly characterised by its lilac brown to dark brown pileus, crowded lamellae with the presence of lamellulae and furcations, stipe often turning reddish-yellow when bruised, subreticulate basidiospores ornamentation and clavate hymenial cystidia often with capitate appendage whose contents change to reddish black in sulphovanillin. It can differ from *R. cyanoxantha* in shorter hymenial cystidia and wider cuticular terminal cells and differ from *R. fusiformata* in frequently present lamellulae and furcations, clavate hymenial cystidia on lamellae edges that have no reaction in sulphovanillin and occasionally branched cuticular hyphal terminations.

Holotype. CHINA, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Lufeng City, G30).

Etymology. ‘*lilaceofusca*’ refers to a lilac brown pileus.

Description. *Basidiomata* medium-sized; pileus 40–60 mm in diameter, initially hemispherical when young, convex to applanate after mature; margin incurved, no striation, not cracked; surface dry, glabrous, reddish-white (8A2), lilac (15B4), brown (7E5) to dark brown (7F5). **Lamellae** adnate, very crowded, 20–24 per cm near pileus margin, cream, unchanging when bruised; lamellulae present and irregular in length; furcations frequently present; edge entire and concolorous. **Stipe** 35–50 $\times$ 8–17 mm, cylindrical to subcylindrical, slightly expanded towards the base, white (1A1), staining reddish-yellow (4A6) when touched, solid. **Context** white (1A1), unchanging when bruised, soft; taste mild; odour inconspicuous. **Spore print** not observed.

Basidiospores $(6.5-7.0-7.8-8.7(-10.5) \times (5.5-6.1-6.9-7.7(-9.4) \mu\text{m})$, $Q = (1.05-1.09-1.13-1.17(-1.26))$, subglobose to broadly ellipsoid; ornamentation of small to medium, dense (5–9 in a $3 \mu\text{m}$ diam. circle) amyloid warts, less than $0.5 \mu\text{m}$ high, subreticulate, connected by short line connections or ridges; suprahilar plage large, inamyloid. **Basidia** $(26.5-30.5-38.5-47.0(-56.0) \times (9.5-10.5-12.5-14.0(-15.5) \mu\text{m})$, clavate or ellipsoid, 1- to 4-spored, thin-walled; basidiola clavate or ellipsoid, ca. $8.0-13.0 \mu\text{m}$ wide. **Hymenial cystidia on lamellae sides** dispersed to moderately numerous, $(39.5-43.5-48.5-$

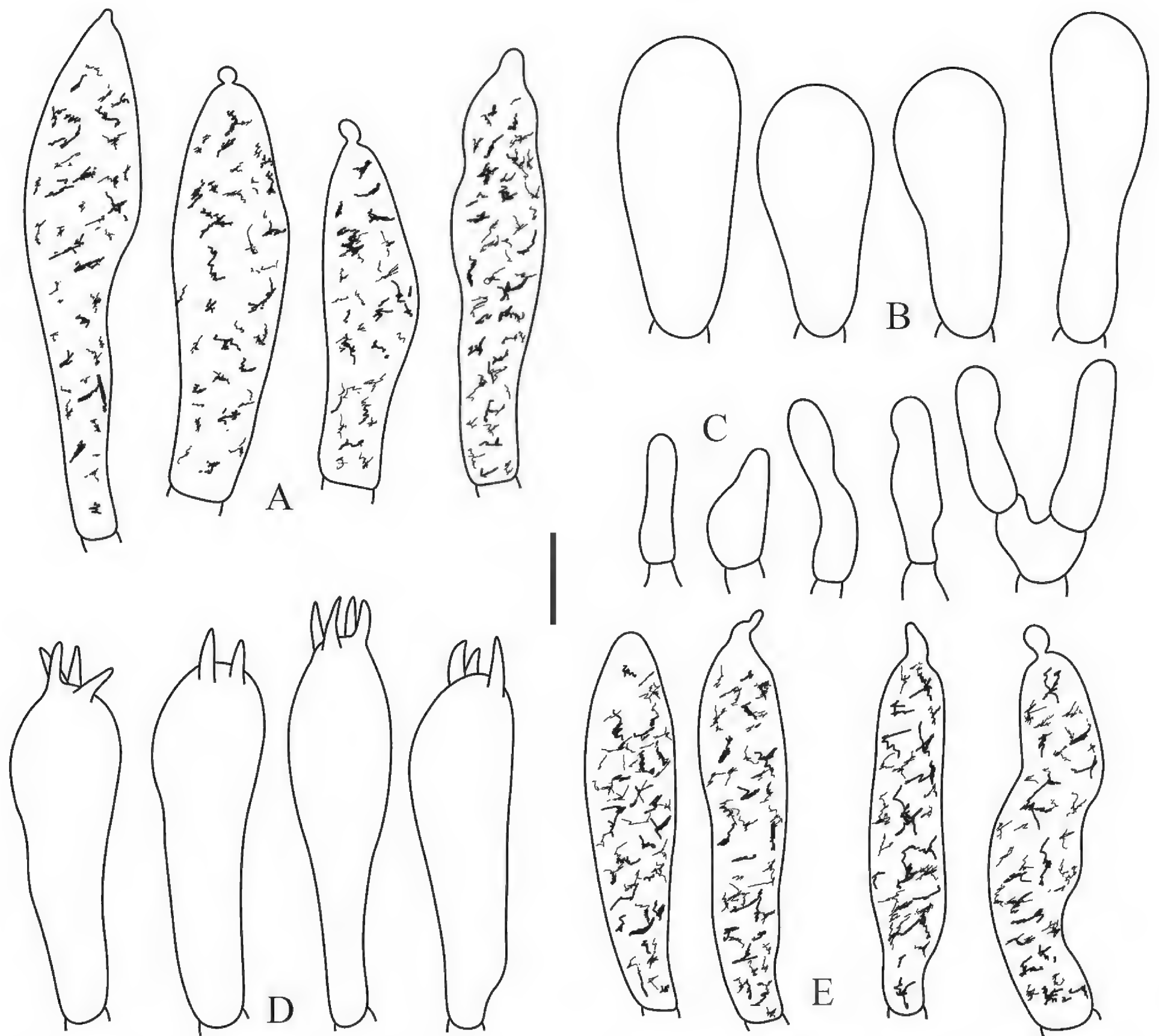


Figure 8. *Russula lilaceofusca* (RITF6330, holotype) **A** hymenial cystidia on lamellae sides **B** basidiola **C** marginal cells **D** basidia **E** hymenial cystidia on lamellae edges. Scale bar: 10 μm .

53.5(–60.0) $\times$ (8.0–)9.5–10.5–11.5(–12.0) μm , mostly clavate, apically mostly obtuse, often with a 2.0–4.5 μm round appendage, thin-walled; contents granulose or heteromorphous, reddish-black in sulphovanillin. **Hymenial cystidia on lamellae edges** shorter and narrower than those on lamellae sides, (31.0–)36.0–41.5–47.0(–54.0) $\times$ (7.0–)7.5–8.5–10.0(–10.5) μm , mostly clavate, apically mostly obtuse, occasionally with a 2–3 μm long round or elliptical appendage, thin-walled; contents heteromorphous, reddish-black in sulphovanillin. **Marginal cells** (13.5–)15.0–18.5–22.0(–26.0) $\times$ 4.0–5.0–5.5(–6.5) μm , lageniform, clavate or subcylindrical. **Pileipellis** only hyphae of suprapellis metachromatic in cresyl blue, sharply delimited from the underlying context, two-layered, gelatinised; suprapellis 130–200 μm deep, composed of loosely arranged and erect hyphal terminations; subpellis 90–200 μm deep, composed of horizontally orientated and intricate hyphae. Hyphal terminations near the pileus margin occasionally branched, thin-walled, often flexuous; terminal cells (11.0–)12.5–18.5–24.0(–32.0) $\times$ (3.0–)3.5–4.0–5.0(–5.5) μm , mainly lageniform or cylin-

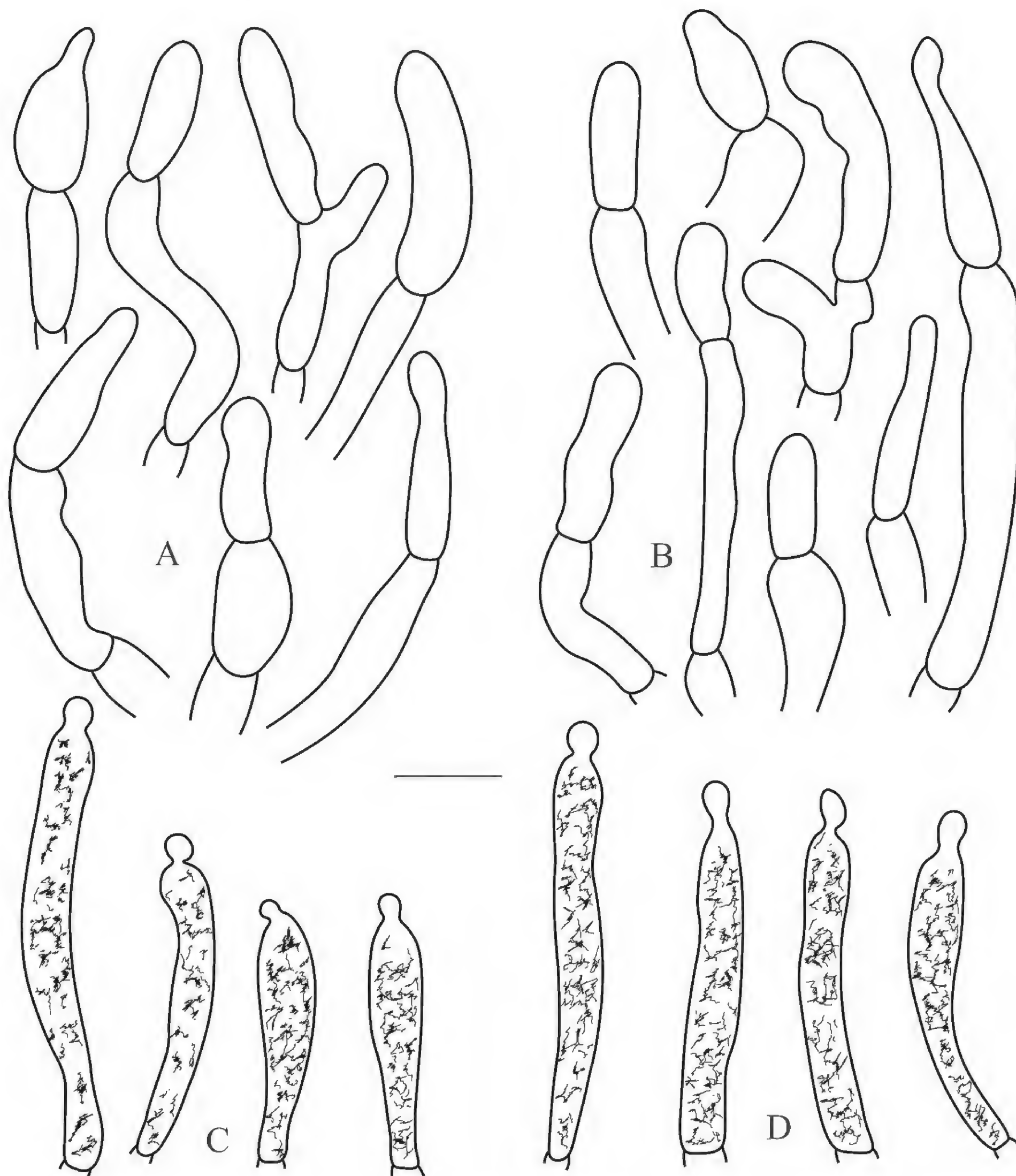


Figure 9. *Russula lilaceofusca* (RITF6330, holotype) **A** hyphal terminations near the pileus margin **B** hyphal terminations near the pileus centre **C** pileocystidia near the pileus margin **D** pileocystidia near the pileus centre. Scale bar: 10 µm.

drical, apically obtuse, sometimes attenuated or constricted; subterminal cells usually longer and slightly wider, ca. 3.5–7.0 µm wide, occasionally branched. Hyphal terminations near the pileus centre slightly shorter than those near the pileus margin; terminal cells (9.5–)11.5–16.0–20.0(–25.5) × (3.0–)3.5–4.0–5.0(–5.5) µm, lageniform or cylindrical, apically obtuse, sometimes attenuated or constricted; subterminal cells usually equal or slightly wider, ca. 2.8–6.6 µm,

occasionally branched. ***Pileocystidia*** near the pileus margin always 1-celled, (23.5–)26.5–35.0–43.5(–51.0) × (3.5–)4.0–4.5–5.5 µm, subfusiform or cylindrical, apically usually obtuse, always with 2–3 µm long, round or elliptical appendage, thin-walled; contents heteromorphous, reddish-black in sulphovanillin. Pileocystidia near the pileus centre similar to those near the pileus margin, (30.5–)34.5–39.5–44.5(–53.0) × 3.5–4.0–4.5(–5.5) µm.

Habitat. On the ground of broad-leaved forests dominated by *Quercus* spp. or mixed forests with *Pinus* spp.

Known distribution. Central (Hubei Province) and south-western China (Guizhou and Yunnan Provinces).

Additional specimens examined. CHINA, Guizhou Province, Zunyi City, Kuan-kuoshui National Nature Reserve, 28°14'29"N, 107°11'59"E, alt. 1750 m, 27 Sep 2014, H.J. Li (RITF3761); Hubei Province, Shennongjia Forest District, Jianglongping, 31°25'46"N, 110°20'18"E, alt. 1500 m, 9 Aug 2015, Y.K. Li (RITF2645); ibid, 11 Aug 2015, Y.K. Li (RITF2631).

Note. Phylogenetic analyses showed that *R. lilaceofusca* was closely related to the Indian species *R. lakhanpalii* and *R. variata* from the United States. However, *R. lakhanpalii* differs in having a yellowish-white to pale yellow areolate pileus with orange-brown centre, cystidia that show no change in sulphovanillin and longer and wider pileocystidia of (27.0–)40.0–63.0–86.5(–123.0) × (4.0–)4.5–5.5–6.5(–7.0) µm near the pileus margin (Ghosh et al. 2020). *Russula variata* differs in having a green pileus and basidiospores with higher warts of 0.4–1.0 µm (Hessler 1960; Burge 1979). In morphology, Chinese *R. fusiformata* Y. Song can be easily confused with this species. However, *R. fusiformata* can be distinguished by its striate pileus margin, absence of lamellulae and furcations, fusiform hymenial cystidia on the lamellae edges, cystidia that show a negative reaction in sulphovanillin and unbranched terminal cells in the pileipellis (Song 2022). *Russula lilaceofusca* is similar to *R. cyanoxantha*, but *R. cyanoxantha* has a greenish-violet pileus, longer hymenial cystidia up to 100 µm and slender cuticular hyphal end cells of 2–3 µm (Romagnesi 1967; Bon 1988; Sarnari 1998).

***Russula perviridis* Y.L. Chen, B. Chen & J.F. Liang, sp. nov.**

MycoBank No: 851266

Figs 2J–L, 3M–R, 10, 11

Diagnosis. *Russula perviridis* is characterised by its large basidiomata, smooth pileus surface, frequently present lamellulae and furcations, a coarser stipe with yellow-brown tinge, globose to broadly ellipsoid basidiospores with locally reticulate ornamentation, long hymenial cystidia that turn greyish-black in sulphovanillin and is symbiotic with *Quercus semecarpifolia*. It differs from *R. dinghuensis* in longer and wider hymenial cystidia on lamellae edges, subreticulate basidiospores ornamentation and is associated with *Quercus semecarpifolia*. It differs from *R. nigrovirens* in frequently present furcations, subreticulate basidiospores ornamentation, longer and wider hymenial cystidia and related host plants.

Holotype. CHINA, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri La County, Bitahai Nature Reserve, 27°49'42"N, 99°59'30"E, alt. 3600 m, 20 Aug 2014, Q. Zhao (RITF3131).

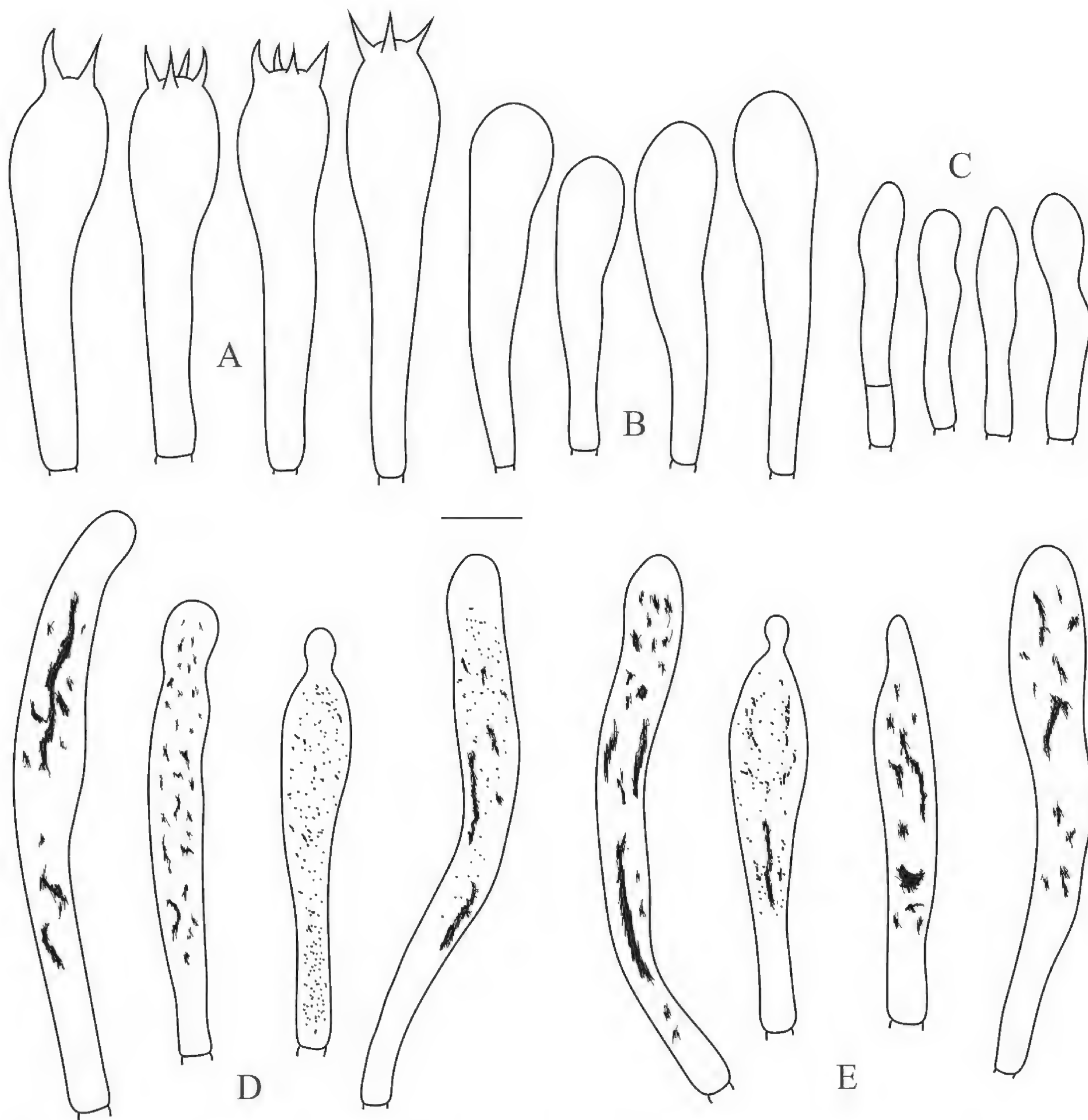


Figure 10. *Russula perviridis* (RITF3131, holotype) **A** basidia **B** basidiola **C** marginal cells **D** hymenial cystidia on lamellae sides **E** hymenial cystidia on lamellae edges. Scale bar: 10 μ m.

Etymology. '*perviridis*' refers to a dark green pileus.

Description. **Basidiomata** large-sized; pileus 90–150 mm in diameter, initially hemispherical to when young, applanate with a depressed centre when mature; margin usually incurved, striation short or inconspicuous, cracked when mature; surface dry, smooth and glabrous, peeling readily, greyish-green (27E5–30C5) to dark green (30F5), sometimes yellow-brownish (2C5) near the centre, greyish-yellow (2C3) or greenish-white (26A2) at the margin. **Lamellae** adnate to subfree, 9–12 per cm near pileus margin, white to cream, staining yellowish-brown (5E6) when bruised, 6–8 mm wide; lamellulae present and irregular in length; furcations frequently present near the stipe to half of the lamellae;

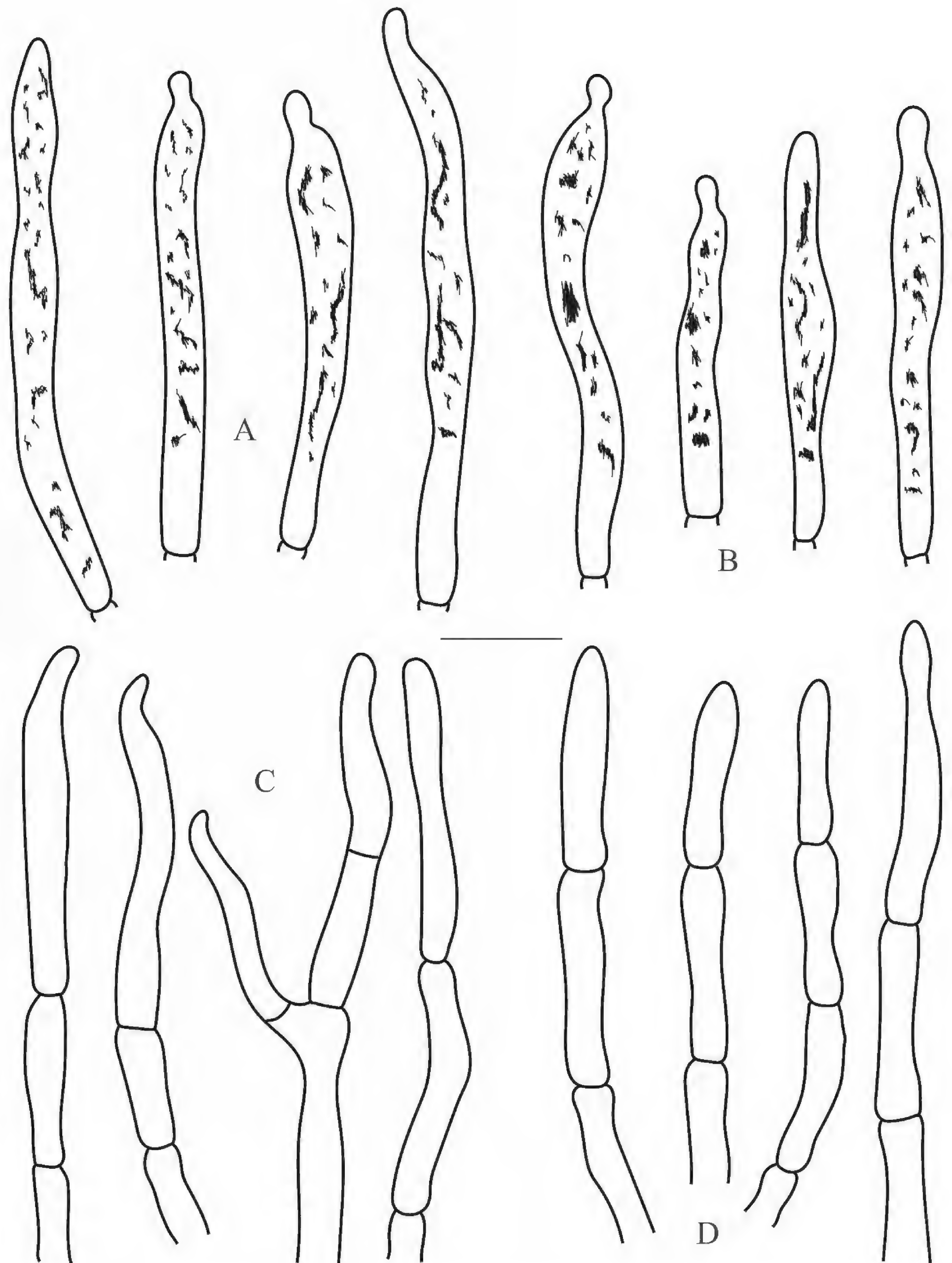


Figure 11. *Russula perviridis* (RITF3131, holotype) **A** pileocystidia near the pileus margin **B** pileocystidia near the pileus centre **C** hyphal terminations near the pileus margin **D** hyphal terminations near the pileus centre. Scale bar: 10 µm.

edge entire and concolorous. **Stipe** 70–90 × 20–40 mm, cylindrical, white (1A1) with yellow-brown (2C5) tinge, solid. **Context** white (1A1), unchanging when bruised, 4–9 mm thick in half of the pileus radius, relatively soft; taste mild; odour inconspicuous. **Spore print** not observed.

Basidiospores (5.9–)7.1–7.7–8.3(–9.7) × (5.2–)6.1–6.8–7.4(–8.4) µm, $Q = (1.00\text{--})1.07\text{--}1.14\text{--}1.21(–1.31)$, globose to broadly ellipsoid, hyaline in 5% KOH; ornamentation of small, dense (5–10 in a 3 µm diam. circle) amyloid warts, less than 0.5 µm high, reticulate, connected by short line connections or ridges; suprahilar plage large, inamyloid. **Basidia** (26.0–)34.5–42.0–59.0(–55.0) × (8.0–)9.5–11.0–12.0(–13.0) µm, clavate, 2- to 4-spored, thin-walled; basidiola clavate, ca. 6–11 µm wide. **Hymenial cystidia on lamellae sides** moderately numerous, (56.5–)62.5–69.5–77.0(–81.5) × (6.5–)7.0–7.5–8.0 µm, fusiform or clavate, apically mostly obtuse, sometimes acute, thin-walled; contents heteromorphous, greyish-black in sulphovanillin. **Hymenial cystidia on lamellae edges** similar to those on lamellae sides, (45.0)54.0–64.5–74.5(–79.5) × 6.0–7.5–8.5(–10.0) µm, mostly clavate, occasionally fusiform, apically mostly obtuse, sometimes with 3–5 µm long appendage, thin-walled; contents granulose or heteromorphous, greyish-black in sulphovanillin. **Marginal cells** (23.0–)24.5–27.5–33.5 × (4.5–)5.5–6.0–7.0 µm, clavate or subcylindrical, occasionally flexuous. **Pileipellis** only hyphae of suprapellis weakly metachromatic in cresyl blue, sharply delimited from the underlying context, 300–360 µm deep, two-layered, not gelatinised; suprapellis 180–200 µm deep, composed of erect and densely arranged hyphal terminations; subpellis 140–180 µm deep, composed of horizontally orientated, intricate and 3–5 µm wide hyphae. Hyphal terminations near the pileus margin occasionally branched, thin-walled, sometimes flexuous; terminal cells (17.0–)20.0–25.5–31.5(–38.0) × 3.0–4.0–4.5(–6.0) µm, usually clavate or subcylindrical, apically tapering; subterminal cells usually shorter, ca. 4–6 µm wide, occasionally branched. Hyphal terminations near the pileus centre shorter than those near the pileus margin; terminal cells (13.0–)14.5–20.5–26.5(–32.0) × 3.5–4.0–4.5 µm. **Pileocystidia** near the pileus margin always 1-celled, (36.5–)40.5–47.5–55.0(–60.0) × (3.0–)3.5–4.0–4.5 µm, fusiform or subcylindrical, apically usually obtuse, sometimes with 2–6 µm long, round or elliptical appendage, thin-walled; contents heteromorphous or granulose, greyish-black in sulphovanillin. Pileocystidia near the pileus centre similar to those near the pileus margin, (26.5–)28.0–36.0–44.0(–50.5) × 3.0–3.5–4.5 µm.

Habitat. On the ground under broad-leaved forests dominated by *Quercus semecarpifolia*.

Known distribution. South-western (Sichuan and Yunnan Provinces) and western China (Xizang Autonomous Region).

Additional specimens examined. CHINA, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Daocheng County, Yading Village, 4 Aug 2022, X.L. He (RITF6734); Yunnan Province, Diqing Tibetan Autonomous Prefecture, Deqin County, Wudi Lake, 27°48'47"N, 99°42'50"E, alt. 3300 m, 11 Sep 2023, Y.L. Chen & J.Y. Liang (RITF6982, 6983); Shangri La City, Bita Sea Scenic Area, 27°49'39"N, 99°59'28"E, alt. 3600 m, 15 Jul 2014, Q. Zhao (RITF3143); Xizang Autonomous Region, Linzhi City, Motuo County, 29°22'13"N, 95°26'59"E, alt. 1800 m, 15 Jul 2014, Q. Zhao (RITF2912); Lhasa City, Mozhugongka County, Zhaxigang Township, 29°42'10"N, 92°4'44"E, alt. 4500 m, 7 Aug 2023, Y. Zhang (RITF6790).

Notes. Phylogenetic analyses showed that *R. perviridis* is related to two European species, *R. langei* Bon and *R. cyanoxantha* and the Chinese species *R. nigrovirens*. However, *R. langei* has a violaceous pileus, a white stipe with a lilac tinge and narrower cuticular hyphal terminations (2.0–3.0 µm) (Bon 1988), whereas *R. cyanoxantha* has non-reticulate basidiospore ornamentation and longer hymenial cystidia up to 100 µm (Bon 1988; Sarnari 1998). *Russula nigrovirens* differs in having patches on the pileus surface, furcations rarely present near the stipe, basidiospore ornamentation that does not form a reticulum and smaller hymenial cystidia (46.0–55.0 × 6.5–8.5 µm) on the lamellae edges (Zhao et al. 2015). Morphologically, *R. perviridis* has a green pileus as in Chinese *R. dinghuensis* J.B. Zhang & L.H. Qiu. However, *R. dinghuensis* differs in its shorter and narrower hymenial cystidia on lamellae edges (45.0–52.0 × 4.0–6.0 µm) and isolated basidiospore warts (Zhang et al. 2017). Furthermore, *R. perviridis* can be clearly distinguished from similar *Cyanoxanthinae* species in its habitat. *Russula perviridis* is distributed in subalpine areas (over 2,000 m) and is associated with *Quercus semecarpifolia*. However, *R. nigrovirens* is associated with *Picea* spp., *Rhododendron* spp., *Sorbus* spp. and *Abies* spp. and *R. dinghuensis* is distributed in low-altitude areas (below 1,000 m).

Key to known species in *R.* subsect. *Cyanoxanthinae* in Asia

- 1 Lamellulae absent or rare 2
- Lamellulae irregularly inserted, but frequent (more than usual in subg. *Heterophyllidiae*).....4
- 2 Association with *Pinus merkusii*.....3
- Association with Fagaceae.....***R. fusiformata***
- 3 Lamellae and context changing pale purplish-pink when bruised, hymenial cystidia on lamellae edges numerous and short (35.0–57.5 × 10.0–10.5 µm).....***R. lilacina***
- Lamellae and context unchanging when bruised, hymenial cystidia on lamellae edges dispersed to moderately numerous and long (45.0–77.5 × 7.5–10.0 µm).....***R. purpureoviridis***
- 4 Basidiospores ornamentation mainly subreticulate to reticulate 5
- Basidiospores ornamentation mainly isolated.....7
- 5 Lamellae instant (9–12/cm at pileus margin), average length of hymenial cystidia on lamellae edges over 50 µm***R. perviridis***
- Lamellae crowded to very crowded (14–27/cm at pileus margin), average length of hymenial cystidia on lamellae edges less than 50 µm 6
- 6 Hymenial cystidia on lamellae sites short and wide of (39.5–)43.5–48.5–53.5(–60.0) × (8.0–)9.5–10.5–11.5(–12.0) µm, clavate, pileocystidia near the pileus margin short and narrow [(23.5–)26.5–35.0–43.5(–51.0) × (3.5–)4.0–4.5–5.5] µm***R. lilaceofusca***
- Hymenial cystidia on lamellae sites short and wide of (45–)47.2–548.5–61.8(–75) × (6–)6.6–7.3–7.9(–8) µm, cylindrical to subclavate to fusiform, pileocystidia near the pileus margin long and wide [(27–)39.8–63.1–86.5(–123) × (4–)4.4–5.4–6.4(–7)] µm***R. lakhampalii***
- 7 Lamellae furcations absent or rare 8
- Lamellae furcations irregularly inserted, but frequent (more than usual in subg. *Heterophyllidiae*).....12

- 8 Appearing in subalpine forest dominated by *Picea* spp., *Rhododendron* spp., *Sorbus* spp. and *Abies* spp. ***R. nigrovirens***
- Appearing in evergreen broad-leaved forest dominated by *Shorea robusta*, *Lithocarpus corneus*, *Quercus* spp. **9**
- 9 Hymenial cystidia on lamellae edges narrow (not exceeding 7 µm wide) ..
..... ***R. dinghuensis***
- Hymenial cystidia on lamellae edges wide (most cells exceeding 7 µm wide)..... **9**
- 10 Basidiospores broadly ellipsoid to ellipsoid, occasionally subglobose.....
..... ***R. lotus***
- Basidiospores subglobose to broadly ellipsoid..... **11**
- 11 Lamellae adnate, context unchanging when bruising or with FeSO₄, hymenial cystidia on lamellae edges short (36–64.5 × 7.2–10.8 µm), pileocystidia short and narrow (18.2–32 × 3.5–5.4 µm)..... ***R. pseudocyanoxantha***
- Lamellae adnexed to subdecurrent, context changing light yellow when bruising or with FeSO₄, hymenial cystidia on lamellae edges long (54–60–95 × 7–8.5–10 µm), pileocystidia short and narrow (17–53 × 4.5–9 µm) ..
..... ***R. purpureorosea***
- 12 Basidiospores globose to subglobose (Q < 1.15) ***R. banwatchanensis***
- Basidiospores subglobose to ellipsoid (Q = 1.15–1.45) **13**
- 13 Basidiospores broadly ellipsoid to ellipsoid (Q = 1.30–1.45).....
..... ***R. subpallidirosea***
- Basidiospores subglobose to broadly ellipsoid (Q = 1.15–1.30) **14**
- 14 Pileocystidia often with moniliform appendage ***R. phloginea***
- Pileocystidia with capitate appendage **15**
- 15 Pileal margin tuberculate-striate, lamellae distant (5–8/cm near the pileus margin), hymenial cystidia on lamellae edges long and wide [(54.5–)58.0–65.0–71.5(–75.5) × (8.0–)9.0–10.5–11.5(–13.0)] µm, fusiform, cuticular hyphal terminations branched..... ***R. atrochermesina***
- Pileal margin indistinctly or not striate, lamellae slightly crowded (10–13/cm near the pileus margin), hymenial cystidia on lamellae edges short and narrow [(35.0–)39.1–45.8–52.5(–56.0) × (6.0–)7.0–8.1–9.2(–10.0)] µm, mostly clavate or subcylindrical, cuticular hyphal terminations unbranched ***R. lavandula***

Discussion

Our multi-gene phylogenetic analyses (Fig. 1) indicate that species with white spore print, basidiospores ornamented by warts with inamyloid suprahilar spot, metachromatic pileipellis and one-celled pileocystidia constitute subsect. *Cyanoxanthinae*. The analyses also suggest that *Cyanoxanthinae* can be divided into two major lineages, which may be distinguishable by the connections of basidiospores ornamentation. Clade 1 represented by *R. lilaceofusca* and *R. perviridis* has more connections between the warts. Clade 2 represented by *R. lavandula* and *R. atrochermesina* has more isolated warts. Additional studies are need to determine the critical point for the number or density of connections. There are no other morphological differences that can clearly correspond to these two lineages.

We recommend several main characteristics that can be used to distinguish species within *Cyanoxanthinae*. The first, lamellulae and furcations are

crucial characters in our view. Except for *R. fusiformata* having completely regular lamellae, the remaining species in *Cyanoxanthinae* have inserted lamellulae or furcations. The density of lamellulae and furcations may require our attention in future research. The second, the species of *Cyanoxanthinae* have different shape of basidiospores (Q values). Four Chinese species, *R. dinghuensis*, *R. nigrovirens*, *R. lotus* and *R. subpallidirosea* have ellipsoid basidiospores ($Q > 1.3$), while other species have broadly ellipsoid basidiospores ($Q < 1.3$).

The subsect. *Cyanoxanthinae* is a widely distributed group, ranging from tropical forests to temperate regions and have formed ectomycorrhizal relationships with various host plants. All known species come from the Northern Hemisphere, except for one species from Madagascar. Australia is an unexplored continent for studying this group. For the level of species, there seems to be restricted life zones and specific hosts. For example, we found that *R. perviridis* is only distributed in the subalpine zone and only forms a symbiotic relationship with *Quercus semecarpifolia*. The European *R. cyanoxantha* is well-known to many people in China. Despite our team conducting surveys in the southern provinces of China (subtropical regions) for over a decade, we have not found it there. This means it is a strictly temperate species.

Currently, it is known that there are 16 species in the subsect. *Cyanoxanthinae* distributed in Asia, including the four new species described in this article. These species are all found from tropical or subtropical regions and, so far, there have been no new species found from temperate Asia. In view of the wide distribution of members of the subsection in Europe, more attention needs to be paid to temperate Asia.

Amongst the 12 known species in China, we can only confirm that *R. phloginea* is edible and more support is needed for the edibility of the remaining species.

Acknowledgements

We are very grateful to the following people for providing us with examined specimens: Dr Y.J. Hao (Anhui Agricultural University), Dr X.L. He (Sichuan Academy of Agricultural Sciences), Dr H.J. Li (The Chinese Center for Disease Control and Prevention), Dr Q. Zhao (Kunming Institute of Botany, Chinese Academy of Sciences) and Ms Y. Zhang (China Telecom Corp Ltd).

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was supported by the National Natural Science Foundation of China (No. 32370018 and 32300010) and the National Non-profit Institute Research Fund of the Chinese Academy of Forestry (CAFYBB2019ZA001).

Author contributions

Writing the original draft: Yanliu Chen; improving the manuscript: Junfeng Liang; providing fund projects: Junfeng Liang and Bin Chen; collecting studied specimens: Yanliu Chen, Bin Chen, Ruoxi Liang, Shengkun Wang, Mengya An, Jinhua Zhang, Jingying Liang, Yaxin Wang and Xuelian Gao. All authors have read and agreed to the published version of the manuscript.

Author ORCIDs

Yanliu Chen  <https://orcid.org/0000-0002-8054-2517>

Bin Chen  <https://orcid.org/0000-0001-8459-3752>

Shengkun Wang  <https://orcid.org/0000-0002-2487-6344>

Mengya An  <https://orcid.org/0009-0001-6170-5886>

Jinhua Zhang  <https://orcid.org/0000-0001-8523-644X>

Jingying Liang  <https://orcid.org/0000-0003-4111-4859>

Yaxin Wang  <https://orcid.org/0009-0002-1302-5154>

Xuelian Gao  <https://orcid.org/0009-0006-6059-4877>

Junfeng Liang  <https://orcid.org/0000-0002-0433-2577>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

- Adamčík S, Looney BP, Caboň M, Jančovičová S, Adamčíková K, Avis PG, Barajas M, Bhatt RP, Corrales A, Das K, Hampe F, Ghosh A, Gates G, Kälviäinen V, Khalid AN, Kiran M, De Lange R, Lee H, Lim YW, Kong A, Manz C, Ovrebo C, Saba M, Taipale T, Verbeken A, Wisitrassameewong K, Buyck B (2019) The quest for a globally comprehensible *Russula* language. *Fungal Diversity* 99(1): 369–449. <https://doi.org/10.1007/s13225-019-00437-2>
- Bon M (1988) Clé monographique des russules d'Europe. *Documents Mycologiques* 18: 1–120.
- Burge HA (1979) Basidiospore structure and development in the genus *Russula*. *Mycologia* 71(5): 977–995. <https://doi.org/10.1080/00275514.1979.12021102>
- Buyck B (1989) Valeur taxonomique du Bleu de Cresyl pour le genre *Russula*. *Bulletin de la Société Mycologique de France* 105: 1–6.
- Buyck B, Hofstetter V, Eberhardt U, Verbeken A, Kauff F (2008) Walking the thin line between *Russula* and *Lactarius*: The dilemma of *Russula* subsect. *Ochricompactae*. *Fungal Diversity* 28: 15–40.
- Buyck B, Zoller S, Hofstetter V (2018) Walking the thin line... ten years later: The dilemma of above- versus below-ground features to support phylogenies in the Russulaceae (Basidiomycota). *Fungal Diversity* 89(1): 267–292. <https://doi.org/10.1007/s13225-018-0397-5>
- Buyck B, Wang XH, Adamčíková K, Caboň M, Jančovičová S, Hofstetter V, Adamčík S (2020) One step closer to unravelling the origin of *Russula*: Subgenus *Glutinosae* subg. nov. *Mycosphere* 11(1): 285–304. <https://doi.org/10.5943/mycosphere/11/1/6>
- Buyck B, Horak E, Cooper JA, Wang XH (2024) *Russula* subgen. *Cremeoochraceae* subgen. nov.: A very small and ancient lineage sharing with *Multifurca* (Russulaceae) an identical, largely circum-Pacific distribution pattern. *Fungal Systematics and Evolution* 14: 109–126. <https://doi.org/10.3114/fuse.2024.14.07>

- Caboň M, Eberhardt U, Looney BP, Hampe F, Kolařík M, Jančovičová S, Verbeken A, Adamčík S (2017) New insights in *Russula* subsect. *Rubrinae*: Phylogeny and the quest for synapomorphic characters. *Mycological Progress* 16(9): 877–892. <https://doi.org/10.1007/s11557-017-1322-0>
- Caboň M, Li GJ, Saba M, Kolarik M, Jancovicova S, Khalid AN, Moreau PA, Wen HA, Pfister DH, Adamcik S (2019) Phylogenetic study documents different speciation mechanisms within the *Russula globispora* lineage in boreal and arctic environments of the Northern Hemisphere. *IMA Fungus* 10(1): 5. <https://doi.org/10.1186/s43008-019-0003-9>
- Crous PW, Boers J, Holdom D, Osieck, Steinrucken TV, Tan YP, Vitelli JS, Shivas RG, Barrett M, Boxshall A-G, Broadbridge J, Larsson E, Lebel T, Pinruan U, Sommai S, Alvarado P, Bonito G, Decock CA, De la Peña-Lastra S, Delgado G, Houbraken J, Maciá-Vicente JG, Raja HA, Rigueiro-Rodríguez A, Rodríguez A, Wingfield MJ, Adams SJ, Akulov A, AL-Hidmi T, Antonín V, Arauzo S, Arenas F, Armada F, Aylward J, Bellanger J-M, Berraf-Tebbal A, Bidaud A, Boccardo F, Cabero J, Calleda F, Corriol G, Crane JL, Dearnaley JDW, Dima B, Dovana F, Eichmeier A, Esteve-Raventós F, Fine M, Ganzert L, García D, Torres-Garcia D, Gené J, Gutiérrez A, Iglesias P, Istel Ł, Jangsantear P, Jansen GM, Jeppson M, Karun NC, Karich A, Khamsuntorn P, Kokkonen K, Kolařík M, Kubátová A, Labuda R, Lagashetti AC, Lifshitz N, Linde C, Loizides M, Luangsa-ard JJ, Lueangjaroenkit P, Mahadevakumar S, Mahamedi AE, Malloch DW, Marinowitz S, Mateos A, Moreau P-A, Miller AN, Molia A, Morte A, Navarro-Ródenas A, Nebesářová J, Nigrone E, Nuthan BR, Oberlies NH, Pepori AL, Rämä T, Rapley D, Reschke K, Robicheau BM, Roets F, Roux J, Saavedra M, Sakolrak B, Santini A, Ševčíková H, Singh PN, Singh SK, Somrithipol S, Spetik M, Sridhar KR, Starink-Willemse M, Taylor VA, van Iperen AL, Vauras J, Walker AK, Wingfield BD, Yarden O, Cooke AW, Manners AG, Pegg KG, Groenewald JZ (2022) Fungal Planet description sheets: 1383–1435. *Persoonia - Molecular Phylogeny and Evolution of Fungi* 48: 261–371. <https://doi.org/10.3767/persoonia.2022.48.08>
- De Crop E, Nuytinck J, Van de Putte K, Wisitrassameewong K, Hackel J, Stubbe D, Hyde KD, Roy M, Halling RE, Moreau PA, Eberhardt U, Verbeken A (2017) A multi-gene phylogeny of *Lactifluus* (Basidiomycota, Russulales) translated into a new infrageneric classification of the genus. *Persoonia* 38(1): 58–80. <https://doi.org/10.3767/003158517X693255>
- Ghosh A, Das K, Bhatt RP, Hembrom ME (2020) Two new species of the genus *Russula* from western Himalaya with morphological details and phylogenetic estimations. *Nova Hedwigia* 111(1–2): 115–130. https://doi.org/10.1127/nova_hedwigia/2020/0588
- Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hessler LR (1960) A study of *Russula* types. *Memoirs of the Torrey Botanical Club* 21: 1–59.
- Khatua S, Paloi S, Acharya K (2021) An untold story of a novel mushroom from tribal cuisine: An ethno-medicinal, taxonomic and pharmacological approach. *Food & Function* 12(10): 4679–4695. <https://doi.org/10.1039/D1FO00533B>
- Kornerup A, Wanscher JH (1981) *Taschenlexikon der Farben*, 3rd edn. Muster-Schmidt Verlag, Göttingen.
- Kropp BR (2016) Russulaceae in American Samoa: New species and further support for an Australasian origin for Samoan ectomycorrhizal fungi. *Mycologia* 108(2): 405–413. <https://doi.org/10.3852/15-171>

- Li F, Deng QL (2018) Three new species of *Russula* from South China. *Mycological Progress* 17(12): 1305–1321. <https://doi.org/10.1007/s11557-018-1447-9>
- Looney BP, Ryberg M, Hampe F, Sanchez-Garcia M, Matheny PB (2016) Into and out of the tropics: Global diversification patterns in a hyperdiverse clade of ectomycorrhizal fungi. *Molecular Ecology* 25(2): 630–647. <https://doi.org/10.1111/mec.13506>
- Looney BP, Meidl P, Piatek MJ, Miettinen O, Martin FM, Matheny PB, Labbe JL (2018) Russulaceae: A new genomic dataset to study ecosystem function and evolutionary diversification of ectomycorrhizal fungi with their tree associates. *The New Phytologist* 218(1): 54–65. <https://doi.org/10.1111/nph.15001>
- Matheny PB (2005) Improving phylogenetic inference of mushrooms with *RPB1* and *RPB2* nucleotide sequences (Inocybe; Agaricales). *Molecular Phylogenetics and Evolution* 35(1): 1–20. <https://doi.org/10.1016/j.ympev.2004.11.014>
- Nuhn ME, Binder M, Taylor AFS, Halling RE, Hibbett DS (2013) Phylogenetic overview of the Boletineae. *Fungal Biology* 117(7–8): 479–511. <https://doi.org/10.1016/j.funbio.2013.04.008>
- Nylander JAA (2004) MrModeltest v2. Program Distributed by the Author; Evolutionary Biology Centre, Uppsala, Uppsala University.
- Romagnesi H (1967) Les Russules d'Europe et d'Afrique du Nord. Bordas, Paris.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Sarnari M (1998) Monografia illustrata del Genere *Russula* in Europa, Vol. 1. A.M.B. Fondazione centro studi micologici, Vicenza.
- Smith SA, Dunn CW (2008) Phyutility: A phyloinformatics tool for trees, alignments and molecular data. *Bioinformatics* 24(5): 715–716. <https://doi.org/10.1093/bioinformatics/btm619>
- Song Y (2022) Species of *Russula* subgenus *Heterophyllidia* (Russulaceae, Basidiomycota) from Dinghushan Biosphere Reserve. *European Journal of Taxonomy* 826: 1–32. <https://doi.org/10.5852/ejt.2022.826.1831>
- Song J, Liang JF, Mehrabi-Koushki M, Krisai-Greilhuber I, Ali B, Bhatt VK, Cerna-Mendoza A, Chen B, Chen ZX, Chu HL, Corazon-Guivin MA, da Silva GA, De Kesel A, Dima B, Dovana F, Farokhinejad R, Ferisin G, Guerrero-Abad JC, Guo T, Han LH, Ilyas S, Justo A, Khalid AN, Khodadadi-Pourarpanahi S, Li TH, Liu C, Lorenzini M, Lu JK, Mumtaz AS, Oehl F, Pan XY, Papp V, Qian W, Razaq A, Semwal KC, Tang LZ, Tian XL, Vallejos-Tapullima A, van der Merwe NA, Wang SK, Wang CQ, Yang RH, Yu F, Zapparoli G, Zhang M, Antonin V, Aptroot A, Aslan A, Banerjee A, Chatterjee S, Dirks AC, Ebrahimi L, Fotouhifar KB, Ghosta Y, Kalinina LB, Karahan D, Liu J, Maiti MK, Mookherjee A, Nath PS, Panja B, Saha J, Sevcikova H, Voglmayr H, Yazici K, Haelewaters D (2019) Fungal Systematics and Evolution: FUSE 5. *Sydowia* 71: 141–245. <https://doi.org/10.12905/0380.sydowia71-2019-0141>
- Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22(21): 2688–2690. <https://doi.org/10.1093/bioinformatics/btl446>
- Swofford DL (2003) Phylogenetic analysis using parsimony and other methods. Version 4. Sinauer Associates, Sunderland, Massachusetts.

- Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* Species. *Journal of Bacteriology* 172(8): 4238–4246. <https://doi.org/10.1128/jb.172.8.4238-4246.1990>
- Wang J, Buyck B, Wang XH, Bau T (2019) Visiting *Russula* (Russulaceae, Russulales) with samples from southwestern China finds one new subsection of *R.* subg. *Heterophyllidia* with two new species. *Mycological Progress* 18(6): 771–784. <https://doi.org/10.1007/s11557-019-01487-1>
- White TJ, Bruns T, Lee SJ, Taylor JL (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *PCR protocols* 18: 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Zhang JB, Li JW, Li F, Qiu LH (2017) *Russula dinghuensis* sp. nov. and *R. subpallidirosea* sp. nov., two new species from southern China supported by morphological and molecular evidence. *Cryptogamie. Mycologie* 38(2): 191–203. <https://doi.org/10.7872/crym/v38.iss2.2017.191>
- Zhao Q, Li YK, Zhu XT, Zhao YC, Liang J-F (2015) *Russula nigrovirens* sp. nov. (Russulaceae) from southwestern China. *Phytotaxa* 236(3): 249–256. <https://doi.org/10.11646/phytotaxa.236.3.5>

Supplementary material 1

ITS

Authors: Yanliu Chen, Bin Chen, Ruoxi Liang, Shengkun Wang, Mengya An, Jinhua Zhang, Jingying Liang, Yaxin Wang, Xuelian Gao, Junfeng Liang

Data type: fas

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/mycokeys.107.123304.suppl1>

Supplementary material 2

LSU

Authors: Yanliu Chen, Bin Chen, Ruoxi Liang, Shengkun Wang, Mengya An, Jinhua Zhang, Jingying Liang, Yaxin Wang, Xuelian Gao, Junfeng Liang

Data type: fas

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/mycokeys.107.123304.suppl2>

Supplementary material 3

RPB2

Authors: Yanliu Chen, Bin Chen, Ruoxi Liang, Shengkun Wang, Mengya An, Jinhua Zhang, Jingying Liang, Yaxin Wang, Xuelian Gao, Junfeng Liang

Data type: fas

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/mycokeys.107.123304.suppl3>

Supplementary material 4

SSU

Authors: Yanliu Chen, Bin Chen, Ruoxi Liang, Shengkun Wang, Mengya An, Jinhua Zhang, Jingying Liang, Yaxin Wang, Xuelian Gao, Junfeng Liang

Data type: fas

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/mycokeys.107.123304.suppl4>